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BREEDING CROP PLANTS

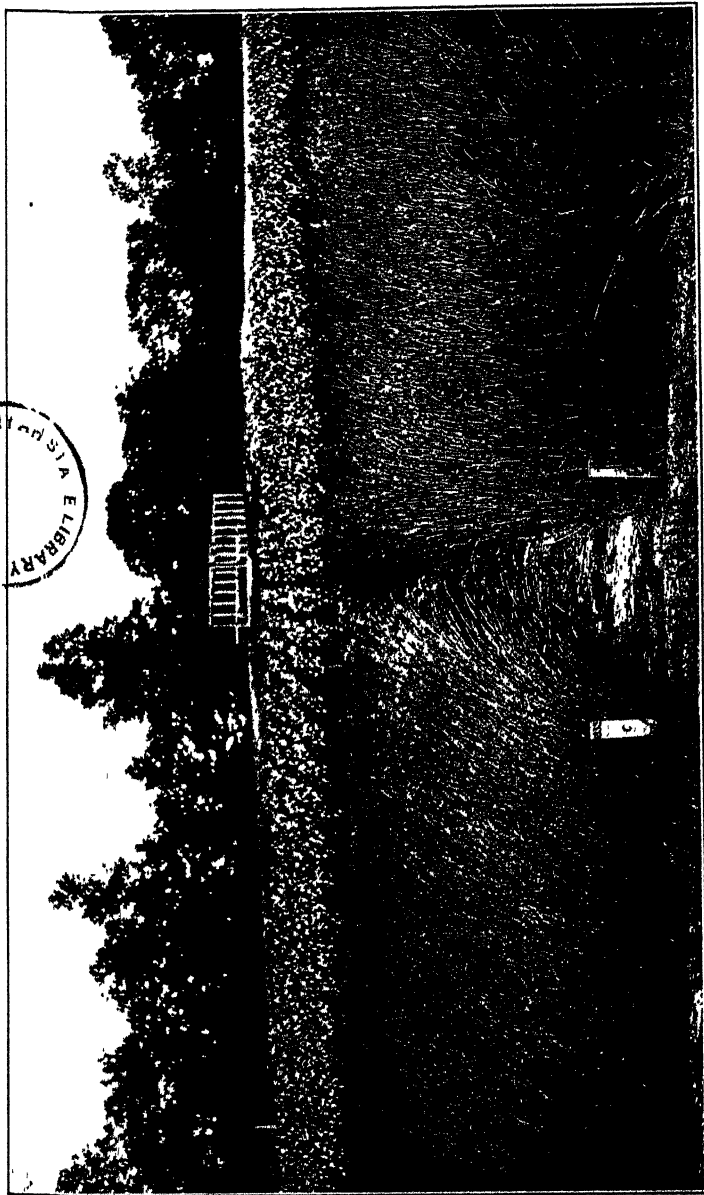
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Improved and commercial strains of timothy At the left, commercial timothy variety, and at the right, one of the improved types produced by Cornell University. (*Courtesy of Myers.*)

(*Frontis piece*)

BREEDING CROP PLANTS

BY

HERBERT KENDALL HAYES

*Professor of Plant Genetics and Chief of Division of Agronomy and Plant
Genetics, College of Agriculture, University of Minnesota*

AND

RALPH JOHN GARBER

*Professor and Head of the Department of Agronomy and
Genetics, West Virginia University*

SECOND EDITION

EIGHTH IMPRESSION

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To
EDWARD MURRAY EAST

PREFACE TO SECOND EDITION

The production of improved varieties of crop plants is of outstanding importance in the development of a more efficient agriculture. A knowledge of laws of heredity, biometrical tools, field and laboratory technic, together with an understanding of the genetics of the particular crop which is being studied are an absolute necessity for the trained breeder. The present volume aims to furnish reliable information in these various lines.

The new edition was necessary because of the rapid advancement in the field of pure and applied genetics which has materially modified methods of breeding certain categories of crop plants. The method of breeding cross-pollinated plants by means of selection in self-fertilized lines has been featured together with a discussion of the effects of self-fertilization in various cross-pollinated plants. The experiences of the writers, in cooperation with plant pathologists, in breeding disease-resistant varieties of plants have led to the inclusion of most of the important literature in this field.

Knowledge of chromosome numbers and relationships has furnished a reliable means for the determination of taxonomic relationships of some crop plants and has given suggestive hints as to their origin, and also has furnished information regarding the practical possibilities of obtaining improvement through species crosses. The new edition summarizes the most recent advances in this field. A knowledge of the mode of inheritance of all characters of the various crops is desirable. Accordingly rather complete summaries of the mode of inheritance of characters are included primarily for reference. The extensive literature on maize genetics is of great importance to the student of pure genetics as well as to the breeder of crop plants. The present edition furnishes the most complete published summary of maize genetics now available. A new chapter on Biometrical Methods has been added and the entire book has been rewritten.

Suggestions from teachers who have used the first edition were of material value and have been freely used. The method of presentation is that which has been developed as a result of over ten years experience in teaching genetics and plant breeding courses to undergraduate and graduate students in the universities of Minnesota and West Virginia.

The writers wish to again express their appreciation to those who gave helpful advice and criticism and whose names were mentioned in the preface of the first edition. Suggestions or aid given at that time

have been of value in the present edition. The writers wish to thank Dr. J. Arthur Harris for helpful suggestions in relation to the chapter on Biometry. Dr. F. J. Krantz has again made helpful suggestions in relation to the chapter on Potato Improvement. Professor John Parker, of the Kansas State Agricultural College, has kindly pointed out numerous small errors in the previous text and made available certain unpublished material regarding sorghum improvement which has been of considerable value. Dr. John H. Martin has likewise made helpful suggestions regarding sorghum. Dr. G. Nilsson-Leissner has aided in calling the attention of the writers to foreign literature and in abstracting certain papers. Particular thanks are due to several of our coworkers. Dr. H. E. Brewbaker, Prof. F. J. Stevenson and Dr. Forrest R. Inner of the University of Minnesota and Prof. M. M. Hoover of the University of West Virginia have read various chapters and aided in checking certain of the calculations. Dr. L. D. Arnett, Librarian, West Virginia University, and Miss Hazel C. Lusebrink kindly helped check some of the literature citations. Miss L. Mac Centerwall has aided in obtaining publications from other libraries and Miss Alma Schweppe has helped make up the index. Prof. F. J. Stevenson has carefully read the entire book and his suggestions have been especially helpful.

Several illustrations have been supplied by investigators who have made intensive studies of particular crops; credit for these has been given in connection with the illustrations. Most of the other figures are from photographs by Mr. T. J. Horton, official photographer at University Farm, St. Paul. Figures on flower structure are from drawings made by Mr. G. D. George, illustrator.

The papers of many investigators have been referred to in the text, as the advanced student will frequently desire to study the original publication. The possibilities of errors are very great in a text which reviews the studies of numerous investigators. The writers, therefore, earnestly invite the criticism of the readers.

UNIVERSITY OF MINNESOTA,

WEST VIRGINIA UNIVERSITY,
June, 1927.

H. K. HAYES.

R. J. CARBER.

PREFACE TO FIRST EDITION

Since the early development of agriculture by primitive peoples, selection of seed for planting has been an important feature of agricultural practice. While many of our better varieties or strains of crop plants have originated as chance seedlings or from selections made by men who lacked a knowledge of the laws of heredity, there has been a growing appreciation in recent years of the value of training students for the occupation of plant breeding.

Studies in crop genetics carried on since 1900, as well as studies in field plot technic, have helped in a large measure to standardize methods of breeding. Information regarding the mode of inheritance of particular characters as well as a better knowledge of the wild relatives of our crop plants is constantly being obtained. The purpose of this book is to present fundamental principles of crop breeding and to summarize known facts regarding the mode of inheritance of many of the important characters of crop plants. Much of the material here presented has been used in courses in crop breeding which have been given in recent years at the College of Agriculture, University of Minnesota.

Suggestions from others in relation to methods of treatment of various subjects have been of material value. Particular mention should be made of the helpful advice of Dr. M. J. Dorsey regarding the chapters on "Plant Genetics" and "Fruit Breeding;" of F. A. Krantz regarding the chapter on "Potato Breeding," and of John Bushnell and W. T. Tapley regarding the chapter on "Vegetable Breeding."

We are also indebted to Miss Alice McFeely, Bulletin Editor, for many suggestions regarding presentation and for assistance in proofreading; to Mr. A. N. Wilcox for assistance in proofreading; to Miss L. Mae Centerwall for help in obtaining a considerable number of publications from other libraries; and to Miss Alma Schweppe for checking the literature citations. Previous summaries of certain phases of plant breeding methods were made available through the kindness of Professor Andrew Boss. The many helpful suggestions made by Dr. C. V. Piper, Consulting Editor of these publications have been of great value.

Several illustrations have been supplied by investigators who have made intensive studies of particular crops; credit for these has been given in connection with the illustrations. Most of the other figures are from photographs by T. J. Horton, official photographer at University Farm, St. Paul. Figures on flower structure are from drawings made by G. D. George, illustrator.

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THE AUTHORS.

UNIVERSITY OF MINNESOTA,
June, 1921.

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BREEDING CROP PLANTS

CHAPTER I

INTRODUCTION

The origin and mode of development of nearly all of the principal cultivated crops is an obscure and much debated subject. This is partly due to the fact that many crops have been grown for hundreds of years and often the same forms are cultivated as were grown in early periods. It is very probable, for example, that the men of the old Stone Age, 50,000 years ago, had some sort of art of agriculture (Dettweiler, 1914). These conclusions have been drawn from old engravings of this period which were made on cavern walls. Wheat and barley were certainly grown in early times. A carving of the upper Paleolithic Age in the Pyrenees mountains shows winter barley such as is now cultivated in that locality.

Dettweiler writes very interestingly of the agriculture of the Lake Dwellers who lived during the period from 4000 to 2000 B.C. He states that the Lake Dwellers of Switzerland cultivated the short-eared, six-rowed barley, *Hordeum sanctum* of the ancients; the dense-eared, six-rowed variety, *H. hexastichon*, L., variety *densum*; two-rowed barley, *H. distichon*; small lake-dwelling wheat, *Triticum vulgare antiquorum*; true club wheat, *T. vulgare compactum*; Egyptian or English wheat, *T. turgidum*, L.; an awnless thick-eared emmer, *T. dicoccum*, Schrank; one-grained wheat, *T. monöcoccum*, L.; meadow (common) millet, *Panicum miliaceum*, L.; club millet, *P. italicum*, L.; and a type of flax, *Linum angustifolium*, which still grows wild in Greece. An excavation was made in the village of Gleichberg, near Romhild, in 1906. On an old fireplace, with remains from the time of the oldest Bronze Age, were found the following seeds: einkorn, spelt, club wheat, and small lake-dwelling wheat, small lake-dwelling barley, vetch, peas, poppy, and possibly apple seeds.

It is not the purpose here to give the historical development of crops except in so far as to show that many were cultivated in very ancient times by primitive peoples by whom many varieties were developed. As some of the varieties which were then grown are in existence today and are cultivated in some regions, an idea of earlier work is obtained.

The work of the Indians with maize will be briefly considered now. Piper speaks of the plan by which seeds of different colors were planted

together in one hill with the thought that this method gave increased yields. It tended to keep the varieties in a heterozygous condition. For several years Squaw Flint from the Indian reservations in Minnesota has averaged as large a yield per acre at University Farm, St. Paul, as the more carefully selected varieties.

These facts should help to give the student of plant breeding some idea of the great accomplishments in plant production in earlier times and to correct possible exaggeration of relative values of the results of recent work. Present-day breeding has achieved great results and will accomplish much more; the foundation, however, was laid many years ago.

THE FOUNDERS OF THE ART OF PLANT BREEDING

The relation between the science and the art of plant breeding is a very interesting subject. Through many years of trials, methods are improved; and a correct knowledge of the fundamentals of the science often does not widely modify the actual practice involved. As a rule,



FIG 1.—The date palm among the Assyrians.

"Design from the palace of Sargon at Khorsabad (eighth century B C.) showing that the male and female flowers of the date palm were clearly distinguished at that time. The worshiper in the middle is carrying a sprig of male or staminate flowers while the one at the right bears female or pistillate blossoms. The drawings should be compared with the photographs of actual flowers. The winged deity at the left, who is usually identified as the Palm God, holds in his hand a cone which is thought to typify the spathe of the male palm, and thus the principle of fertility in general." (After Johnson, 1915.)

scientific principles allow some short cuts in breeding methods and help to eliminate erroneous and useless practices.

As will be constantly emphasized in this work, there is a close relation between the mode of reproduction and the methods of breeding a plant.

A knowledge of sexuality was, therefore, almost a necessity before it was possible to develop the art of breeding. Sexual processes, while not thoroughly understood, were observed in animals three or four centuries B.C. by the Egyptians and Assyrians. Existence of fruit-bearing and sterile trees of the date palm was known to the people of Egypt and Mesopotamia in early times, and records of artificial pollination as early as 700 B.C. have been found (see Fig. 1). The Assyrians commonly referred to the date trees as male and female. The Greeks, however, to whom early scientific thought is attributed, failed to interpret this phenomenon. Theophrastus, for example, concludes that as other plants do not as a rule exhibit the same phenomenon, the date tree is *not* an example of real sexuality (Johnson, 1915).

Little was actually known of plant sexual processes until comparatively recent times. The English physician, Grew (1676), further developed the suggestion of Sir Thomas Millington that the stamens served as the male organs, by a hypothesis regarding the process of fertilization. The only means of demonstrating this phenomenon was by the experimental method.

The First Demonstration of Sex in Plants.—Camerarius first made the experimental test by using isolated female plants of the mulberry, by emasculating the castor bean and by removing the stigmas from Indian corn. The results of these experiments were reported in a letter to Professor Valentin, of Giessen, written in 1694.

The following statement, made by Camerarius and found in *Ostwald's Klassiker* (p. 25) has been frequently quoted (Johnson, 1915).

In the vegetable kingdom there is accomplished no reproduction by seeds, that most perfect gift of nature, and the usual means of perpetuating the species, unless the previously appearing apices of the flower have already prepared the plant therefor. It appears reasonable to attribute to these anthers a nobler name and office of male sexual organs.

Further Proof of Plant Sexuality.—The work of Camerarius was confirmed by several men. Thomas Fairchild, in 1719, produced a new variety of pinks by an artificial crossing of two varieties; and Bradley, 2 years earlier, found emasculated tulips set no seed. Miller (1731) noted insects pollinating emasculated tulips after first visiting untreated tulip flowers. Governor Logan of Pennsylvania, in 1739, experimented with maize and observed that detasseled plants set no seed when isolated from untreated plants. He also removed the silks and found such treated plants were incapable of setting seed. Gleditsch (1750) had a pistillate palm in Berlin which was 80 years old and had set no seed. He obtained a quantity of pollen from trees in Leipsic (then 9 days' journey from Berlin) and after pollination seed was produced which germinated.

The Studies of Koelreuter.¹—While these investigators and others confirmed the work of Camerarius, little advance was made in the art of breeding until Koelreuter (1761–1766) made a careful study of artificial crosses and gave the first extended account. In tobacco crosses, for example, he found that the first generation was of intermediate habit and, therefore, showed the effect of the male parent. His work on the vigor of first generation crosses is of much interest. He believed the “oil” of the pollen grain after mixing with the stigmatic fluid penetrated the ovule. The belief of a union of male and female substances was a



FIG. 2.—Male and female flowers of date palm about two times natural size. (*Photograph taken by Swingle in Sahara Desert, 1899.*)

step in the right direction. The value of insects as carriers of pollen was also demonstrated.

Early Studies in the Cytology of Fertilization.—Pollen tubes were first observed in 1823 by Amici who followed them to the micropyle of the ovule in 1830. Schleiden shortly afterward made numerous studies of the pollen tube and apparently thought the embryo developed in the embryo sac from the end of the pollen tube. This matter was not thoroughly cleared up until Strasburger (see Johnson, 1915) concluded, in 1884, that:

¹ For these facts the papers of other writers have been freely used. Those by ROBERTS (1919) have been especially helpful.

1. The fertilization process depends upon the copulation with the egg nucleus of the male nucleus which is brought into the egg. 2. The cytoplasm is not concerned in the process. 3. The sperm nucleus, like the egg nucleus, is a true cell nucleus.

An Answer to the Question of Hybrid Fertilization.—Although Koelreuter proved the fact of sexuality in plants, it was not generally accepted, and early in the nineteenth century the Physical Section of the Royal Prussian Academy offered a prize for an answer to the question, “Does hybrid fertilization occur in the plant kingdom?” Among other results presented by Weigmann in answer to this question occurs the statement of the immediate effect of pollen in legumes. Weigmann made a study of 36 crosses using the following plants: onion, cabbage, pea, bean, lentil, pink, and tobacco. He observed the fact of variability due to crossing and thought gardeners should pay more attention to the planting of their crops so that those of like kind did not grow so near each other that crossing through the aid of insects would take place. Sprengel, in a book published in 1793, showed the important rôle played by insects in pollination and studied the adaptations for crossing found in many flowers. He concluded that nature intended that flowers should not be pollinated by their own pollen.

The Great Hybridist Gärtner.—In extent and number of his experiments Gärtner's work is very great. In 1835 he heard of the offer of a prize made by the Dutch Academy of Sciences at Haarlem regarding the place of hybridization in producing new varieties of economic and ornamental plants.

Gärtner's paper on this question, which received the prize, was published in extended form in 1849. He made thousands of crosses, involving nearly 700 species, and obtained about 250 hybrids. The work was so carefully controlled and checked that the fact of sex in plants was thoroughly proved. He made a classification of hybrids according to whether they resembled one or the other parent in all respects, whether they resembled one parent in one part of the plant and the other parent in other characteristics, or whether there was an almost equal balance. In the last case in later generations, the inclination toward the one or the other parent was supposed to be due to a slight overbalance of one or the other of the fertilizing materials. Gärtner explains the appearance of the first hybrid generation as due to an inner force operating according to law. He, like Koelreuter and Weigmann, observed increased vigor in hybrids.

He made experiments to determine the immediate effect of pollen with crosses between colorless and colored pericarp varieties of maize and in crosses between a brown-seeded *Lycchnis* and one with a gray seed. As no change occurred, a law was developed to the effect that pollen does not immediately affect forms and external characters of seeds but influ-

ences the development of the resultant plant. He observed an immediate effect in some pea crosses and learned that the yellow cotyledon color dominated the green in the hybrid seeds

Early English Plant Breeders.—Knight, Goss, and Herbert, three English workers, did much to develop the art of breeding. Knight, who was a practical horticulturist, recognized the aid of artificial cross-pollination in producing new kinds. He studied the question of the immediate effect of pollen. A variety of pea with a white seed coat was fertilized with pollen of a gray-seeded variety. No immediate influence of pollen was obtained. When the resultant plant was pollinated by a white variety, however, both gray- and white-seeded sorts were obtained in the next generation. William Herbert was a contemporary of Knight who learned of the work of Koelreuter some time after he had started his experiments. He opposed the idea that species crosses were necessarily sterile.

Studies made by John Goss are considered of much interest as they showed results similar to those obtained later by Mendel. In 1820 flowers of the Blue Prussian pea, which has bluish seeds, were pollinated with pollen of the Dwarf Spanish. Three seeds were obtained which were yellowish-white like the male parent. Plants grown from the seeds produced some pods with all blue, some with all white, and some with both blue and white seeds in the same pods. When planted, the blue seeds bred true while the white seeds gave some segretates. No law, however, was developed.

Other Workers of This Period.—At about this same period Sargeret, in France, was making studies with *Cucurbitaceæ* crosses. He observed the fact of dominance as the following crosses show:

MUSKMELON (FEMALE)	CANTALOUPE (MALE)	FIRST GENERATION
1. Flesh, white	Flesh, yellow	Flesh, yellow
2. Seeds, white	Seeds, yellow	Seeds, white
3. Skin, smooth	Skin, netted	Skin, netted
4. Ribs, slightly evident	Ribs, strongly pronounced	Ribs, rather pronounced
5. Flavor, sugary and very acid at same time	Flavor, sweet	Flavor, acid

He notes (Roberts, 1919) that:

The characters were not blended or intermediate at all, but were clearly and distinctly those of the one or the other parent.

Naudin made quite careful studies and attempted to summarize his results. He so nearly approached the law later laid down by Mendel that some workers have spoken of it as the Naudin-Mendel law. He thought that if hybrids were self-fertilized they would return more or less rapidly to the parental types. Similar results were obtained if the hybrid was pollinated by one of its parents. He noted the uniformity of the first generation and the production of many types in the second

generation some of which could not be told from the original parents. The results were explained by the segregation of specific substances in the pollen and ovaries of the hybrid (Naudin, 1865).

Wichura (1865) found reciprocal crosses gave like results and, therefore, concluded that the pollen and the egg have exactly the same share in the organism which results from fertilization. He studied species crosses in willows but did not deal with the individual characters of the species.

Mendel's work, published in 1866, is now well known to all students of genetics and plant breeding. With the great advances made since 1900 rules can now be given which furnish a reliable guide for plant-breeding operations. To quote from Pearl:

In the creation of new races by hybridization the plant breeder can and does take Mendelian principles as a direct and immediate guide. He has made Mendelism a working tool of his craft.

THE RELATION OF CERTAIN BIOLOGIC PRINCIPLES TO PLANT BREEDING¹

The art of plant breeding is closely related to those biologic principles which furnish the foundation for the science of breeding. For this reason there is a very close relation between the development of theories of evolution and scientific methods of breeding.

The conception of evolution dates from the time of the Greek philosophers in the eighth century. This was the speculative period and evolutionary beliefs were not attained as a result of experimentation. Until the sciences of botany and zoology were built up, it was impossible to do more than outline theories which appealed to the judgment of the writer.

The modern inductive period is of comparatively recent times. Erasmus Darwin developed a theory of evolution which he did not think entirely adequate. Lamarck gave us the first well-rounded theory of evolution. It was based on the inheritance of acquired characters. By continued use an organ was strengthened and developed. Likewise, without use it was weakened. The supposed inheritance of these acquired characters was the basis of the production of the numerous species.

The term "species" was first applied to animals and plants by John Ray (1628-1705) who used it to refer to a group of organisms with similar characteristics and which freely intercrossed. Many of the experiments of this period dealt with the question of species.

The Doctrine of the Constancy of Species.—Linnaeus (1707-1778) adopted a more strict definition, although he was not always consistent in his use of the word. The doctrine adopted was that of the separate creation of fixed entities which were called species. Lamarck denied this

¹ A bulletin by EAST (1907) and a book by SCOTT (1917) have helped materially and have been freely used.

theory and outlined his evolutionary hypothesis. Most naturalists of this period believed in the immutability of species.

It is thought that the work of Lyell (1797–1875), an eminent geologist, had a marked effect on that of Charles Darwin, who was his intimate friend. Lyell insisted upon the continuity of the history of the earth and the uniformity of agencies which wrought such profound changes upon the earth. This theory was in opposition to that of Cuvier, who believed that the history of the earth was a series of times of destruction followed by periods of tranquillity (“catastrophism”). After each such destructive period it was believed that new creation took place.

Darwin’s Theory of Natural Selection.—The most influential worker in the history of development of the evolutionary conception was Charles Darwin. He and Alfred Russel Wallace independently developed a theory for the origin of species and united in presenting a preliminary paper in 1858.

The publication of Darwin’s “Origin of Species,” in 1859, gradually brought about a belief in evolution. The work of Lyell had helped materially to develop a belief in the orderly progress of the world and assisted in preparing the way for the masterly presentation of Darwin. Darwin presented such a mass of evidence from widely different fields that the entire thinking world was compelled to accept evolution as a fact. The evidence was grouped under such headings as organic relationship, comparative anatomy, embryology, paleontology, and domestication.

The fact of evolution is indisputable. The explanation of the methods of evolution is even yet not entirely satisfactory. Darwin’s theory is founded upon a series of facts as follows:

1. *Variability.*—It is a matter of common observation that no two individuals are exactly alike. If sufficient individuals are examined the range of variation is found to be very great. These variations are universally present.

2. *A Struggle for Existence.*—If all the progeny of some of the lower forms grew to maturity and each in turn produced as many progeny, the world would soon be overrun with a single form. There is competition also between different species and genera.

3. *Natural Selection.*—The conclusion would certainly seem reasonable that those forms would survive which possessed characters better adapted to a given environment and, therefore, gave those particular forms advantage in the struggle for existence.

4. *Heredity.*—Variation produces the material for natural selection to work upon and heredity tends to perpetuate the variations.

The mechanism of transmission of characters, the physiological cause of variations, and the inheritance of different categories of variations were unanswered problems. Many criticisms were made of Darwin’s work and many were considered by Darwin himself. Nearly all of these

have a bearing upon plant breeding. In the improvement of crops, artificial selection takes the place of natural selection. The breeder is constantly faced with the question of the perpetuation of a variation. He also faces the question of whether the useful variation will perpetuate itself in crosses or will be lost.

Darwin recognized two sorts of variations. The "fortuitous" or chance variations are everywhere present and cause every plant to be slightly different from other plants of the same species. These were considered to be of primary importance in evolution. While he recognized "definite" or discontinuous variations, the so-called mutations, these were not considered of primary importance.

The Stability of the Germ Plasm.—Weissmann's theories are of much interest. He developed the idea of the continuity of the germ plasm and that external agencies could not modify inheritance without first affecting the germ cells. Plant breeders are not particularly interested in Weissmann's ingenious theories which were outlined to show that the inheritance of acquired characters was an impossibility. Apparently, in order that a new character may be produced, there must be a modification of the germ plasm. The real question, then, is what causes germinal change? In considering this question we must keep in mind the possibility that agencies which are of little importance from the standpoint of the plant breeder may be of profound importance in evolution.

DeVries' Mutation Theory.—The more recent theory of evolution developed by DeVries attacks the question of the sort of variations which furnish the basis for evolution. DeVries gives only slight value to the small continuous variations and advances the hypothesis that large variations are of primary value. He believes in periods of mutation when from some unknown cause a species is producing many new forms, and other periods when stability of the species is the rule. DeVries recognized three sorts of mutations: (1) progressive, when an entirely new character appears; (2) degressive, the appearance of a partially latent or hidden character; and (3) retrogressive, when an active character becomes latent. The cause, or causes, of these sudden changes was not known. Mutations are frequently not large but small. All sudden heritable changes which cannot be explained by the laws of segregation and recombination are called mutations by present-day geneticists.

The Pure-line Theory.—The studies of Johannsen are of particular value from the standpoint of the plant breeder. He worked with self-fertilized crops and found that while the progeny of a single self-fertilized plant varied quite widely, these variations were not inherited. From single commercial varieties he found it possible to isolate numerous lines which in their means differed slightly from each other and which bred true. Johannsen considered a pure line to be the progeny of one or more self-fertilizations from a single homozygous ancestor. Selection within such

a pure line was of no practical value. Numerous investigations with self-fertilized crops have been made and corroborate the results of Johannsen. Isolated cases of mutations in these pure lines have been reported, and while these are of much scientific interest they occur far too infrequently to be used as a basis for a system of breeding.

Johannsen's pure-line theory has been extended to cover clonal or asexual propagation in both plants and animals. In the proper place evidence will be given to show that in heterozygous organisms which are asexually propagated there sometimes occur bud sports or somatic mutations each of which may form the basis for a new race. Such bud sports in some plants apparently occur frequently enough to be of economic importance.

Mendel's Law of Heredity.—Mendel's experiments, published in 1866, remained unnoticed until the facts were rediscovered in 1900 by DeVries, by Correns, and by Tschermak. This law furnished the starting point from which the modern study of genetics has developed. Many students will have taken a course in genetics before studying plant breeding. For such students it is sufficient, here, briefly to review Mendel's law in its application to crop improvement.

At the time of Mendel's studies the mechanism of Mendelian heredity was unknown. Mendel developed three general laws which were called (1) dominance, (2) unit characters, and (3) segregation. These have been studied intensively in recent years. Dominance is not a general result and frequently the first generation is intermediate in appearance. The unit-character viewpoint has been greatly modified and geneticists now use the term "unit factor." The inheritance of a unit character, as referred to by Mendel, is depended upon a single-factor *difference* in modern genetic usage. A character frequently is the result of the interaction of many factors under the particular conditions of the environment. What is inherited is the manner of reaction rather than the specific character. Segregation appears to be a universal law although the large number of factors involved frequently makes the results very complex.

Mendel worked with seven contrasted character pairs. Among them were yellow cotyledons as contrasted with green, and round seed as contrasted with wrinkled. When a plant with round, yellow cotyledons is crossed with one that has wrinkled, green cotyledons, the first generation or F_1 cotyledons are all round and yellow, since these are the *dominant* characters. If two of the F_1 plants are crossed or an F_1 plant is self-fertilized the next or F_2 generation will be made up of approximately three-fourths round and one-fourth wrinkled seed. This illustrates Mendel's law of *segregation of unit characters* or, in modern genetic terminology, *unit factors*. The factor that differentiates round seed and the one that differentiates wrinkled seed are brought closely together in the F_1 generation but apparently they do not lose their identity because of this

Lab 11

close association as is shown by the fact that they may separate and the F_2 generation become reunited in the several combinations possible, *i.e.*, round with round, round with wrinkled, and wrinkled with wrinkled. If there are approximately equal numbers of round and wrinkled factors, and if the combinations of these as expressed in the F_2 generation are purely at random, the ratio of one-fourth round with round; one-half round with wrinkled; one-fourth wrinkled with wrinkled would be expected. But since round is dominant to wrinkled, it is not possible to distinguish the round-with-round from the round-with-wrinkled combination and, therefore, approximately three-fourths of the F_2 seeds would appear round and one-fourth of the seeds wrinkled. This combination, as a matter of fact, is actually obtained in such a cross.

It is of interest to consider the yellow-green character pair in connection with the round-wrinkled pair. Mendel found that approximately three-fourths of the F_2 round seeds were yellow and one-fourth green and that three-fourths of the F_2 wrinkled seeds were yellow and one-fourth green. It was pointed out that such a result could not be obtained unless the round-wrinkled character pair segregated *independently* of the yellow-green pair. Considering both character pairs at once, the F_2 cotyledons consisted of nine-sixteenths like the dominant parent (round, yellow), one-sixteenth like the recessive parent (wrinkled, green), and three-sixteenths of each of two new combinations (round, green; wrinkled, yellow). This illustrates the principle of independent assortment between different character pairs.

Mendel's law can best be understood in relation to cytology. It is well known that the chromosomes are the bearers of heritable factors. The number of chromosomes for each species is constant and the form and individuality is characteristic. According to Morgan's hypothesis, the factors are located in particular regions or loci of the chromosome. The chromosomes are considered to be in pairs and the two parts of each pair are in such a relation to each other that at reduction division, *i.e.*, at the formation of gametes, the members of each pair separate and the gamete contains only half as much chromatin as the somatic cell. The gamete then contains one member of each chromosome pair. Exceptions to the above rule sometimes occur when unusual cytologic divisions take place.

If there are large numbers of factors and relatively few chromosomes, each chromosome must contain from several to many factors. If each chromosome retained its individuality, the only sort of recombination of factors possible would be those located in different chromosome pairs. As a result of the classical studies of Morgan and his coworkers with *Drosophila*, which have been corroborated by many other geneticists with different organisms, modern theories of linkage and crossing over have been developed. While the mechanism of crossing over is not well understood and there is some dispute over the stage in which crossing

over occurs, the proof of crossing over and recombination of factors between members of the same chromosome pair appears absolute. Factors in the same chromosome show linkage in inheritance, and the closeness of linkage is, in general, correlated with the distance apart of the factors in the chromosome, according to the theory of the linear arrangement of factors.

The present viewpoint is that, at some time in preparation for reduction division, there is a doubling of the spireme and that at this time the members of the same chromosome pair lie next to each other and wind about each other. Cytological proof of such an arrangement is available for some organisms but such an arrangement has not been observed in studies of reduction division with certain other organisms. It is further supposed that at this stage breaks may occur in the chromosomes and that the pieces may reunite in such a manner that a new chromosome is formed which contains parts of each of the homologous chromosomes that make up a pair. This change of location of a factor by which it becomes a part of the other member of the homologous pair of chromosomes is called crossing over.

The importance of crossing over is very great in practical breeding. It allows for a recombination of all factors which are in different loci and are not completely linked although, in order to obtain recombination of closely linked factors, large numbers of individuals must be grown.

Most of the previous investigations show that many factors are inherited independently. This allows for numerous combinations when crosses are made. If there is a break, *i.e.*, a cross-over or some other means by which factors which are partially linked may be recombined, a greater degree of segregation is possible than when factor correlation is absolute.

In general, it may be said that the number of groups of correlated or partially linked factors is not greater than the number of chromosome pairs. Whether or not the above explanation is correct, partly so, or entirely wrong, it is a convenient theory with which to account for a large body of facts. It allows for classification of facts in such a way that correct breeding methods may be used.

Mendel's law may then be summarized from the standpoint of the plant breeder as follows:

1. Plants breed true for certain characters when all factors necessary for the development of the character are in a homozygous condition. There is a relative stability of factors. Changes in factors, or "mutations," are far too infrequent in most higher plants to furnish a basis for a system of breeding.

2. There is independent segregation of certain factors.

3. Partial coupling of certain determiners sometimes is found. The degree of linkage in transmission is quite constant. Crossing over or

recombination of factors within the members of a homologous chromosome pair occurs if the factors are not in similar loci, *i.e.*, absolutely linked.

4. Perfect coupling of certain factors, *i.e.*, constant association of characters in inheritance, occurs. If two characters are absolutely linked, it may be supposed that they are a result of the same factor or factors since it is now realized that a factor frequently modifies the expression of several characters.

As a possible exception to the usual behavior, apparent segregation in the somatic cells of some hybrids may be mentioned. In some forms these changes apparently occur frequently enough to be of practical selective value.

Mendel's law may be summarized in another way by saying that the first generation cross between stable forms may resemble one parent in one character, the other parent in another character; may be intermediate in the character in question; or may exceed one or the other parent. All members¹ of F_1 are of uniform habit. Segregation occurs in F_2 and "segregation of potential characters in the germ cells of hybrids and their chance recombination" (East and Hayes, 1911) may be considered as a general law. In F_3 and later generations, some forms breed true, others segregate.

Homozygous forms may be obtained which contain the desirable characters of both parents. Such forms are as stable as races which have been bred by straight selection.

Hybridization as a Means of Producing Variations.—A quite recent explanation of the cause of germinal variation and, therefore, the main cause of evolution is that of Lotsy (1916), who gives to hybridization the major rôle in the production of variations. Some serious criticisms have been made of this hypothesis as an explanation of evolution. With the higher plants, however, natural crossing has doubtless played an important evolutionary rôle. For the plant breeder crossing is of much importance and it is the *only generally known means of producing variations of selection value that is available as a practical method*. In cross-fertilized species crosses naturally occur followed by segregation, and recombination follows. Selection isolates desirable genotypes.

THE VALUE OF CROP IMPROVEMENT IN RELATION TO A MORE EFFICIENT AGRICULTURE

Maximum yields of crops can be obtained only when all factors relating to the various phases of crop production are favorable. The physical and chemical characteristics of the soil, correct time and rates of planting, and crop rotation must be considered. Recent studies have shown that there are marked differences in the effect of different crops upon those

¹ The meaning of F_1 , F_2 , etc., and other genetic terms not explained in the text is given in the glossary.

that follow them in the rotation. Of utmost importance is the necessity that the crop be adapted to the soil and climatic conditions in which it is to be grown and that profitable returns be obtained on the basis of the cost of production.

After careful consideration of those factors which go to make up the home of the plant, attention may be given to the seed. The fact that there are remarkable differences in final yields from different varieties of the same crop is commonly known. As yet the possibilities of crop improvement have scarcely been realized. Careful methods of seed inspection, registration, and treatment to control diseases are necessary to the greatest return from crop breeding. Education of the farmer will do much to overcome the evils of exploitation by the unscrupulous seed dealer or promoter who is anxious only to sell and make a profit on his seed.

The business of growing carefully bred seeds is one that needs an appreciation of these and other factors in seed production. No great amount of special training is needed to carry on this work. To the careful worker who is willing to build up a reputation by actual merit of his seeds, the business of seed production will prove a lucrative one.

The production of improved forms by breeding is a line of work which demands special training. This can be obtained only from a study of the underlying principles of genetics. Nearly all of the land-grant colleges and experiment stations, as well as some private seed firms, are carrying on studies in plant breeding. Although these studies are yet in their infancy, results of much value are being obtained. By means of accurate field experiments carried on at research stations and with farmer cooperators, the experiment stations and the federal Department of Agriculture are enabled to give accurate information regarding the better varieties to grow. In the past these studies have not always been made with a correct appreciation of the necessary technic.

It is the purpose of this book to outline methods of breeding in relation to the underlying principles involved, and to present what are coming to be recognized as proper field methods of carrying on these studies. Because the subject is a comparatively recent one, new methods of work are constantly being found. It is therefore necessary to present different viewpoints in order that the prospective breeder may learn why certain practices are giving the better results.

CHAPTER II

PLANT GENETICS¹

Since the rediscovery of Mendel's law in 1900, there has been an intensive study of the laws of inheritance through experimental breeding and other means. This has resulted in the development of a new biological science which is called "genetics." A knowledge of the principles of this science is a necessity if the student of crop breeding is to pursue his work in the most logical manner. The writers, therefore, believe that a study of genetics should precede plant breeding. There are, however, many people interested in crop improvement who have not had an opportunity to pursue an intensive study of genetics. For this reason, it seems advisable to present genetic principles in some detail.

Methods of Studying Inheritance of Characters.—The characters of a plant are those qualities which serve to identify it. They are the means whereby one variety is differentiated from another. The production of a variety with only desirable characters is the main aim of the breeder. It is a commonly accepted fact among geneticists that Mendel's law may be used to explain the inheritance of nearly all plant and animal characters. The character is considered to be the end result of the interaction of certain inherited factors which are located in the germ cells; these factors under favorable environmental conditions cause the production of the character. Thus environment and heredity both play important rôles in character development. The laws of inheritance have been developed mainly by controlled crosses between parents of known inheritance. By correlating the facts of character transmission from parent to offspring with known facts of cytology, an idea of the mechanism of heredity has been obtained. Before presenting a description of the factorial scheme which has been developed to explain Mendelian heredity, it will be necessary to give some of the main facts of reproduction in plants.

The Mode of Sexual Reproduction in Flowering Plants.—Nearly all higher plants produce seeds as the result of the union of sexual cells or gametes. Each body cell which is capable of further division contains a nucleus in which the chromatin is located. This chromatin, which is composed of a definite number of parts or chromosomes, gains its name from the fact that it takes a dark stain with certain reagents when other

¹ In preparing this chapter other works on genetics have been freely used. BABCOCK and CLAUSEN (1918) and EAST and JONES (1919) have been particularly helpful.

parts of the cell are unstained. In the soma or body of the plant the nucleus of each cell contains a definite number of chromosomes, half of which were obtained from the male sexual cell and half from the egg cell. Each new body cell results from the longitudinal division of the chromosomes of a preceding body cell. Thus all of the somatic cells of a plant contain the same number of chromosomes.

Preparatory to the formation of the germ cells or gametes, the chromosomes assume a paired condition, one member of each pair being obtained from the male parent and the other from the female parent. At the formation of the sexual cells, or at reduction division, one member

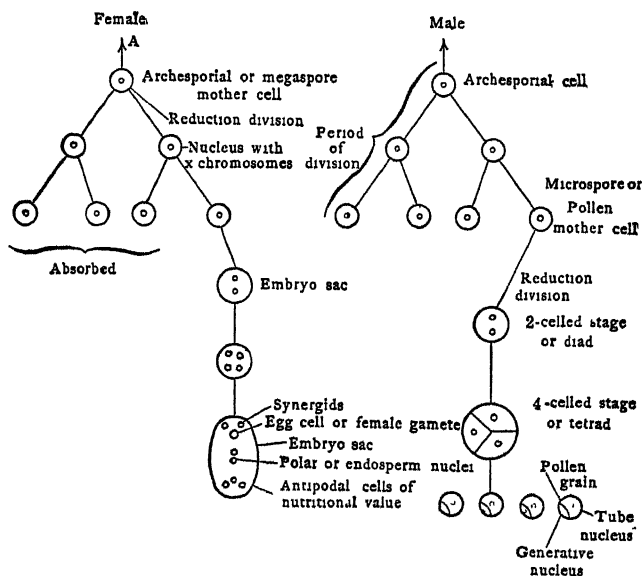


FIG. 3.—Diagram to illustrate production of male and female gametes. A, in some forms as *Lilium* this megaspore mother cell functions directly as the embryo sac. Reduction division in *Lilium* occurs at the first nuclear division within the embryo sac.

of each pair of chromosomes passes to each daughter cell thus reducing the chromosome number to half that in the body cells. Following this reduction division, there is an equating division whereby each chromosome is divided into two qualitatively equal parts. This results in the formation of the male or female sexual cells, or gametes, as they are called (see Fig. 3).

The male sexual cells are produced in the anthers and are carried in the pollen grains. A mature pollen grain contains two nuclei, a tube nucleus and a generative nucleus (see Fig. 4).

After the pollen grain falls on the pistil, the tube cell elongates, forming a pollen tube which passes down the style. This tube grows through the tissue of the pistil and reaches the embryo sac. The generative nucleus passes into the pollen tube and divides, forming two nuclei which

are the male gametes. The pollen tube grows through the tissues of the pistil until it reaches the embryo sac, and the tip of the tube breaks after it penetrates the wall of the embryo sac. In fertilization one of these gametes of the pollen tube unites with the egg cell to form the embryo of the seed and the other unites with two polar nuclei to form the endosperm (see Fig. 5).

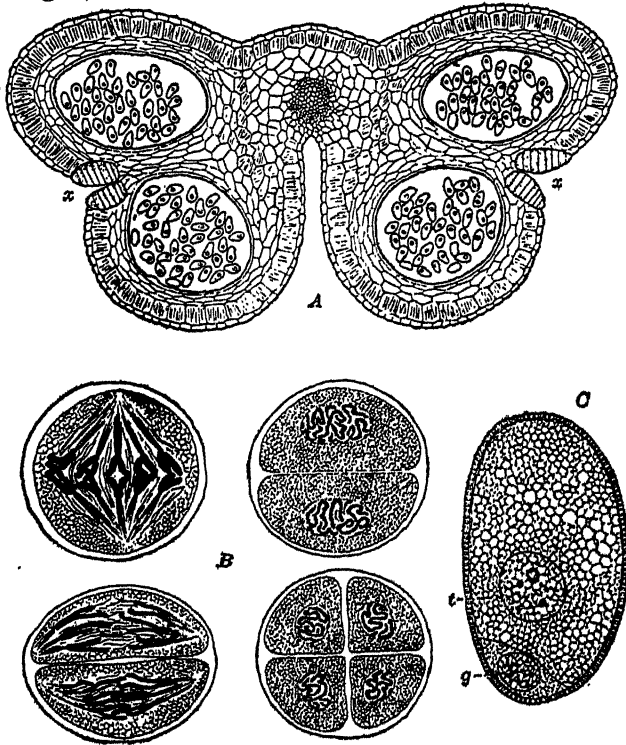


FIG. 4.—Anther and pollen of the lily.

A, mature anther, showing the four locules, or chambers, containing pollen grains; the anther opens lengthwise on both sides along the lines of cells shown at *x*; B, stages in the formation of pollen grains in a group of four (tetrad) within the pollen mother cell; C, mature pollen grain with early stages in the development of the male gametophyte; *t*, tube nucleus; *g*, generative nucleus. (After Bergen and Davis.)

If the chromosome number of each body cell is represented by $2x$, each gamete would be represented by x , the embryo formed by the union of the generative cell with the egg cell would be $2x$ and the endosperm tissue $3x$.

The Inheritance Factors.—Inheritance factors are located in the chromosomes in a linear manner. Each factor, moreover, is considered to be located at a certain definite place or locus of a particular chromosome. The inherited character is the end result of the interaction of specific genetic factors under the conditions of the environment.

In Mendel's original experiments, and in many of the studies conducted in the early years after the rediscovery of Mendel's law in 1900,

the character by which the parents of crosses differed appeared to be dependent upon a single factor pair. In one parent the factors were in a dominant condition and in the other recessive. The F_1 was heterozygous but resembled the dominant parent; in F_2 a simple segregation occurred. This led to the conclusion that many characters were inherited as units. While certain character differences are dependent on a single factor pair, each character is a part of the physiologic complex which goes to make up the organism. Probably, as many recent experiments have proved,

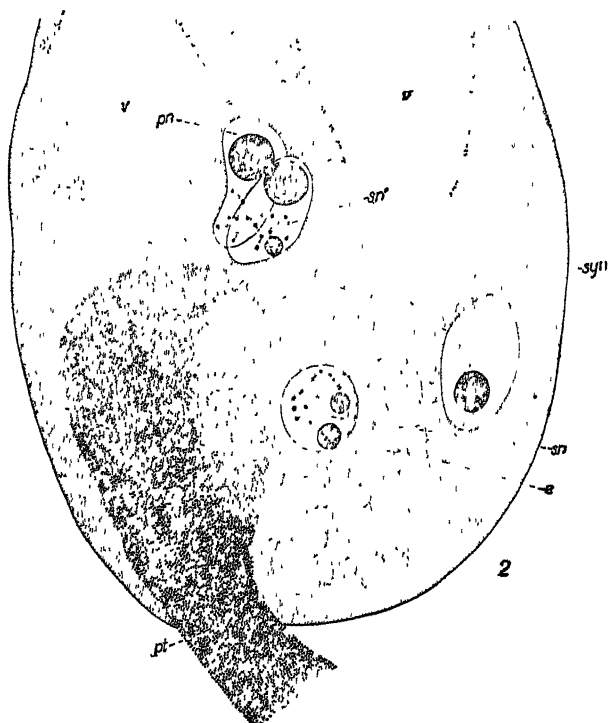


FIG. 5.—Longitudinal section of the lower portion of the embryo sac of maize at the time of fertilization, *pn*, polar nuclei fusing; *sn'*, sperm nucleus fusing with a polar nucleus, *pn*, *e*, egg; *sn*, sperm nucleus in the egg, *pt*, pollen tube; *syn*, synergid, *v*, vacuole (After Miller)

most, if not all, normal characters are the result of the interaction of many genetic factors. When a cross shows that two parents differ by only a single factor, this does not mean that only one genetic factor is necessary for the development of the character. It does mean, however, that a single factor of inheritance may cause a profound change in the expression of the character of an organism. When a plant breeds true for a particular character, each gamete produced contains all factors necessary for the development of the character. These and other facts of genetics are best understood by considering the results of certain crosses.

Before discussing such results it will be desirable to review briefly the subject of variation.

Variability of Characters.—It is commonly recognized that no two plants or animals are exactly alike. These differences are called variations. Several means of classifying variations have been used. For the plant breeder a classification based on inheritance appears of most value. On this basis variations are of two kinds: non-heritable and heritable.

Non-heritable variations, frequently called fluctuations, are due solely to some difference or differences in the environmental conditions under which the plants develop. Heritable variations, sometimes called modifications, are due to some difference or differences in the hereditary characters of the organisms. Either a progeny test, or a study of transmission of the character in suitable crosses, under similar conditions of environment, is the criterion of inheritance.

Several illustrations may help to make clear what is meant by non-heritable variations. Baur (1914) cites races of *Primula sinensis* which under normal conditions breed constantly true for red and white flowers, respectively. If the red race is placed in partial shade in the greenhouse under temperatures of 30 to 35° C., only white flowers are produced. If those same plants are brought into another greenhouse with temperatures of 15 to 20° C., the flowers which then develop are the normal red color. It is pointed out that what this red primula inherits is not a red flower color but the ability to produce a certain flower color under certain conditions of the environment. Non-inherited variations have no value as a means of producing new varieties or strains. Such variations are, however, of importance to the breeder. For example, a small shriveled seed of wheat has the same inherited characters as a large, plump seed of the same pure line. The seedling, nevertheless, produced by the shriveled seed, may get an unfavorable start. A familiar example of non-heritable variation is the difference in height of plants within a variety, which is dependent on differences in food supply, moisture, or sunlight.

Inherited variations may be placed in two classes: (1) mutations, and (2) new combinations.

Mutations are the results of sudden changes in the hereditary mechanism of the organism. They may be the result of a single-factor change, of a change in two or more factors, or of a chromosomal aberration. The causes of such changes are not known for the most part, although in recent years much has been learned regarding chromosomal aberrations. Much more must be learned regarding the nature of hereditary factors before the causes of factor mutations will be determined. Mutations are sometimes of much value to the breeder. Examples of mutations of economic importance will be found under a discussion of the breeding of various crops. When a desirable mutation occurs, it can be utilized as a

means of producing a new race. As there is no known means of artificially inducing favorable inherited variations, the breeder cannot depend upon them as a method of producing improved varieties.

New combinations result from crossing varieties which contain different hereditary factors. The first generation of a cross between homozygous parents which differ in a certain character as a rule will be uniform and may resemble one or the other parent, may be intermediate in habit or a new character expression may be obtained. Second-generation plants, however, will be of different kinds due to the segregation of hereditary factors and their chance recombination in the germ cells of the F_1 plants. When more than a single-factor pair is concerned, new com-

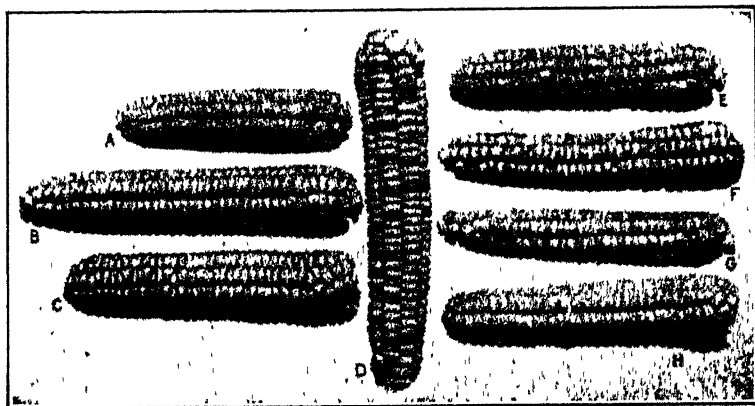


FIG. 6.—Inheritance of starchy and sweet endosperm in maize. A, ear of sweet corn with wrinkled seeds; C, ear of flint corn with starchy seeds; B, immediate result of pollinating ear of starchy parent with pollen from sweet parent, D, produced by self-fertilizing an ear of an F_1 plant of cross between sweet and starchy parent. Note the segregation into sweet and starchy seeds; E, an ear produced by planting wrinkled seeds of D; F, G, H, ears produced by planting starchy seeds of D. Note that one out of every three ears is pure for the starchy character. (After Babcock and Clausen.)

binations of factors may occur and individuals in F_2 and later generations may be produced which have some of the characters of the one parent combined with some characters of the other. In some cases characters which are not present in either parent appear. These may result from the interaction of two or more factors all of which are necessary for the production of the character and part of which were contained in one parent and part in the other. When the factors concerned are located in separate chromosome pairs, their recombination is at random and the result is called independent Mendelian inheritance. When the factors are located in different loci of the same chromosome pair, linkage results, although recombination of factors does occur in many cases. Independent Mendelian inheritance will be illustrated by means of suitable crosses and where the parents differ by one to several pairs of factors.

Monohybrid.—Sweet corn, when mature, bears wrinkled seed, while flint corn produces smooth seeds filled with starch grains. If sweet corn is pollinated with pollen from a flint variety, the resultant seed is starchy. There is an immediate effect due to double fertilization in which the endosperm results from the union of the polar nuclei with one of the gametes of the pollen grain. If the crossed seeds are planted and the resultant plants self-fertilized, the ears produced will contain starchy and sweet seeds in a 3:1 ratio. The facts may be presented by the use of the factor hypothesis. One of the chromosome pairs contains the factors for either the starchy or the sweet condition. Let S represent the sweet factor, F the starchy factor. In the following diagram only one of the chromosome pairs, which contains the starchy and sweet factors, will be shown.

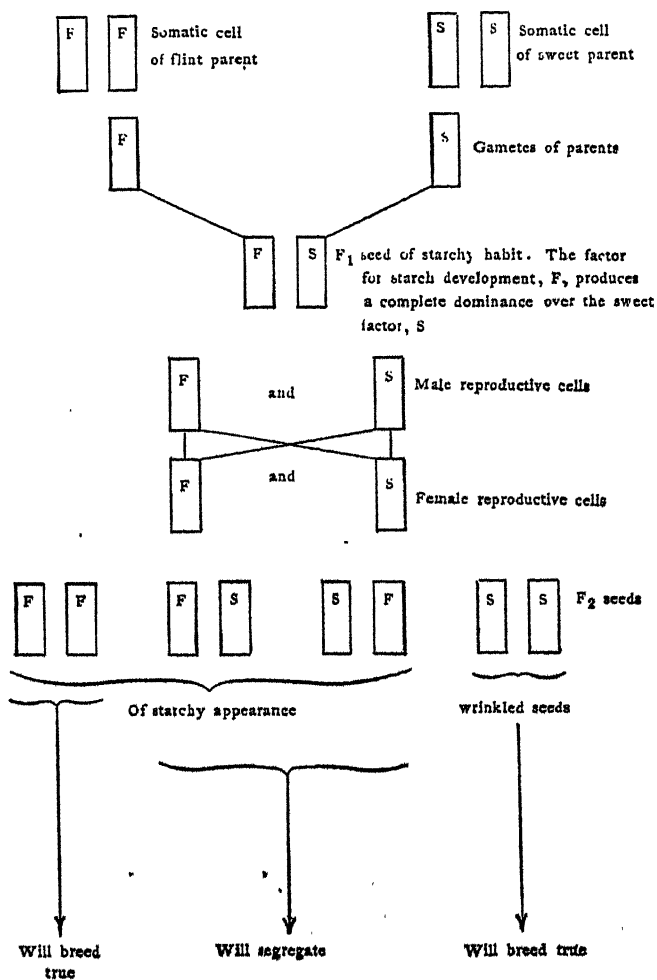


DIAGRAM 1.

Dihybrid.—Crosses between varieties which differ in two independently inherited characters may next be illustrated. The parental forms in the case of each differential character will be considered to differ in only a single inherited factor.

PARENTS	CHARACTERS	GAMETES
White Fife wheat	Awnless spike, white seed	AW
Preston	Bearded spike, red seed	BR

There is a dominance in F_1 of the red-seed color (brownish-red pigment in one of the bran layers) over the white and a partial dominance of the awnless over the bearded condition. The F_1 plants will, therefore, have red seeds and a slight extension of the awns near the top of the spike.

The inherited factors may be considered to be R for red seed, W for white seed, B for bearded, and A for awnless. W and R are considered to be located in homologous loci of one pair of chromosomes and B and A in homologous loci of another pair of chromosomes. The F_1 plants may then be considered as $ABWR$. The gametes of these F_1 plants may contain either A or B in combination with either W or R . The different combinations are supposed to occur in equal frequency.

Wheat (*Triticum vulgare*) has 21 pairs of chromosomes. The factors for bearded or awnless spike and for color of seed are independently inherited. They may be considered, therefore, to be located in separate chromosome pairs. In the diagram only two chromosome pairs are shown.

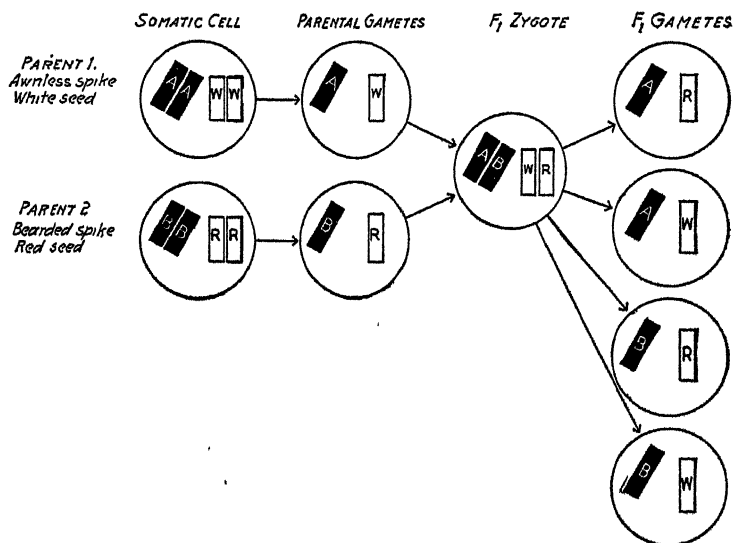


DIAGRAM 2.

The F_2 plants obtained by the self-fertilization of F_1 crosses will then be the result of all possible combinations of the gametes. The combination will be illustrated by the Punnet square.

		Male gametes			
		AR	AW	BR	BW
Female gametes	AR	AR AR	AW AR	BR AR	BW AR
	AW	AR AW	AW AW	BR AW	BW AW
	BR	AR BR	AW BR	BR BR	BW BR
	BW	AR BW	AW BW	BR BW	BW BW

Collecting the various combinations:

	F_2 PLANTS	F_2 BREEDING HABIT
1 AARR	Awnless, red seed.	Will breed true for awnless spike and red seed.
2 ABRR	Int. awns, red seed.	Will segregate for spike character and breed true for red seed.
2 AARW	Awnless, red seed.	Will breed true for awnless spike and segregate for seed color.
4 ABRW	Int. awns, red seed.	Will segregate for both seed color and spike habit.
1 AAWW	Awnless, white seed.	Will breed true for awnless spike and white seed.
2 ABWW	Int. awns, white seed.	Will segregate for spike habit and breed true for white seed.
1 BBBR	Bearded, red seed.	Will breed true for bearded spike and red seed
2 ABBR	Int. awns, red seed.	Will segregate for spike habit and breed true for red seed.
1 BBWW	Bearded, white seed.	Will breed true for bearded spike and white seed.

Several Factors Necessary for the Production of a Character.—In many cases several factors are involved in the production of a single character. Thus the purple aleurone color found in Black Mexican sweet corn is dependent on the interaction of the factors R , C , A , and Pr (see Chap. XV, Maize Inheritance). C and A are basic factors both of which must be present for the development of color. When R , C , and A are present, the color in the aleurone layer is red. Study a cross between Black Mexican which is homozygous for purple aleurone color and a

white sweet which is homozygous for factors *R* and *A* but which lacks the factors *C* and *Pr*. The recessive condition of the factor may be represented by a small letter.

PARENTS	APPEARANCE	GAMETES	F ₁ CROSS
Black Mexican	Purple color	<i>PrRAC</i>	<i>PrprRRAACc</i>
White Sweet.	White color	<i>prRac</i>	

As the *F*₁ seeds contain all factors necessary for the production of purple color in the aleurone layer, they will be purple. In later generations the factors *R* and *A* may be considered to be present in each gamete, as both parents were homozygous for these characters. The gametes of the *F*₁ plants will, therefore, be *PrRAC*, *prRAC*, *PrRac*, and *prRac*. By the Punnet-square method, as illustrated in the previous topic, the student may determine the possible *F*₂ combinations. These will be found to occur in the following proportions:

COMBINATIONS	APPEARANCE
1 <i>PrPrRRAACC</i>	9 Purple aleurone
2 <i>PrprRRAACC</i>	
2 <i>PrPrRRAACc</i>	
4 <i>PrprRRAACc</i>	
1 <i>prprRRAACC</i>	3 Red aleurone
2 <i>prprRRAACc</i>	
1 <i>PrPrRRAAcc</i>	
2 <i>PrprRRAAcc</i>	4 White aleurone
1 <i>prprRRAAcc</i>	

Linkage of Characters in Inheritance.—The brilliant experiments of Morgan and his coworkers with *Drosophila* have led to the development of the present chromosome theory of heredity. Several hundred inherited factors have been studied and their location in the chromosomes determined by their linkage relations. There are four pairs of chromosomes in the fruit fly and four groups of linked factors. A large number of characters are correlated or linked with sex since they are dependent upon factors carried in the X- or sex chromosomes. In normal individuals there are two X- or sex-chromosomes in the female *Drosophila*, and a single X- and a Y-chromosome in the male. There are two other large groups and one very small group of linked factors in *Drosophila*. Correlated genetic and cytologic studies, where one of the small chromosomes was missing, proved that the small group of factors were associated with the small pair of chromosomes. The two large groups of linked factors must then belong to the two pairs of large chromosomes. These three pairs of chromosomes are called autosomes in distinction to the pair of sex chromosomes. Thus in *Drosophila* there are four pairs of chromosomes and four groups of linked factors (Morgan, *et al.*, 1925) (See Fig. 7).

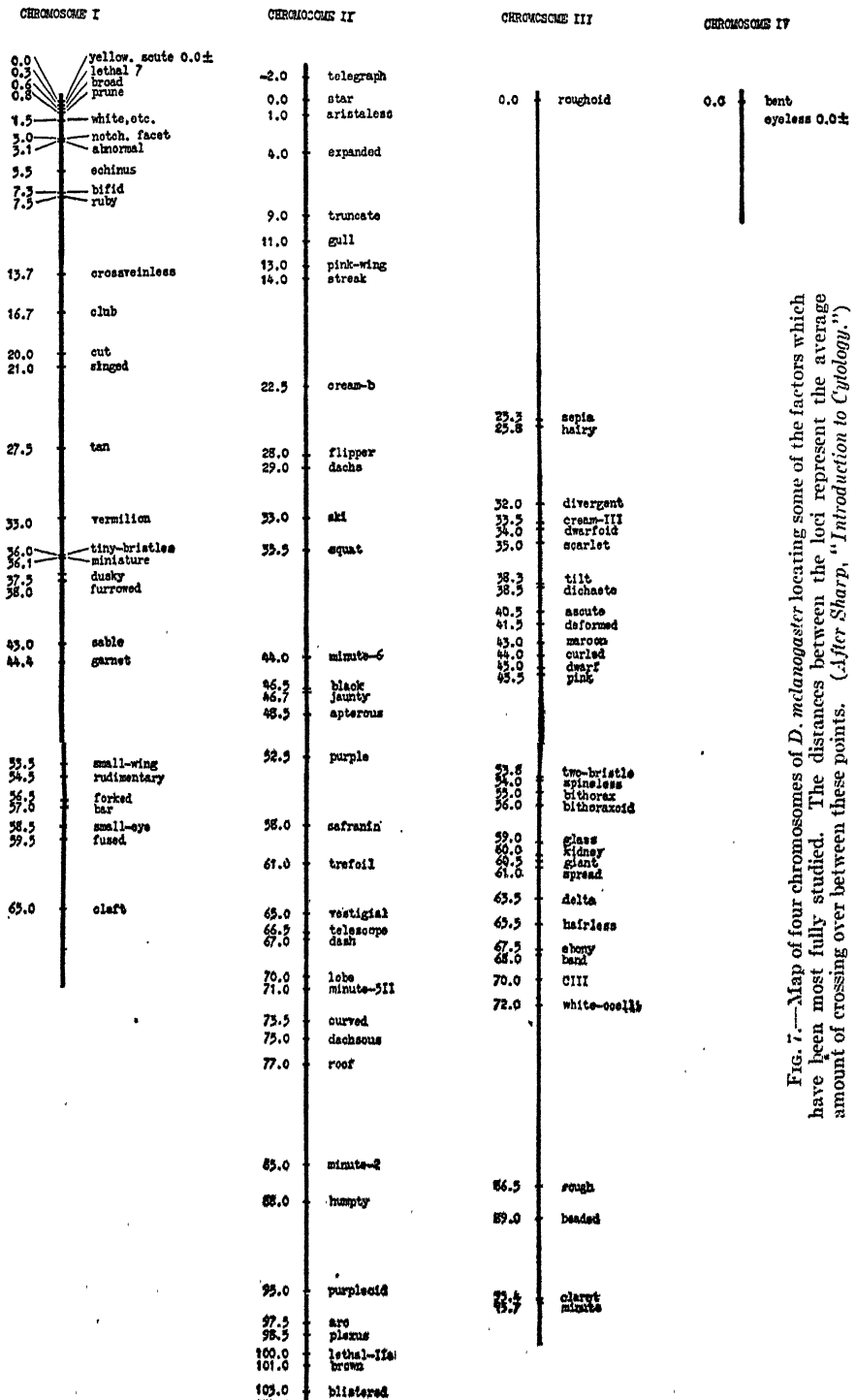


Fig. 7.—Map of four chromosomes of *D. melanogaster* locating some of the factors which have been most fully studied. The distances between the loci represent the average amount of crossing over between these points. (After Sharp, "Introduction to Cytology.")

Many studies of linkage in other organisms have been made and similar principles observed as in *Drosophila*, although data with other organisms are as a rule not extensive enough to furnish complete corroboration of the mechanism worked out with *Drosophila*.

At some stage prior to reduction division, members of a pair of homologous chromosomes lie close together. Jannsen originally observed breaks in members of homologous chromosomes in the thick thread stage which occurred when they were twisted about each other and the mechanism of crossing over has therefore generally been diagrammed as occurring in this stage. Careful studies in *Drosophila* indicate, however, that crossing over in this organism occurs

at a stage at which each parental chromosome has become split into two daughter chromosomes, *i.e.*, at the four strand or tetrad stage, and that crossing over involves two only of the four strands at any given point of crossing over.

It is thought that the only stage at which this could occur regularly is between the last general division and the first maturation division (Morgan, *et al.*, 1925).

Much remains to be learned regarding the mechanism involved but the known facts of crossing over can be appreciated best by reference to an illustration even though that illustration may not indicate correctly the actual period in which crossing over occurs.

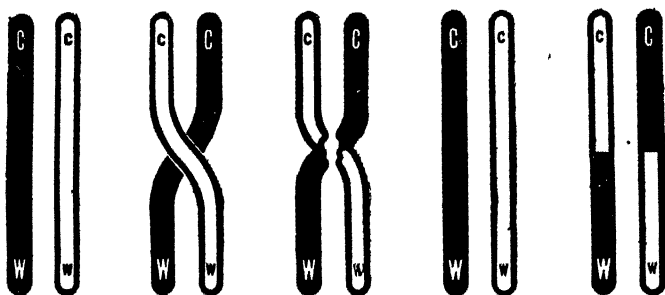


FIG. 8.—Diagrammatic representation of crossing over and results. At the left, the two original chromosomes. In the middle, the twisted condition of the chromosomes in synapsis and their subsequent separation. At the right, the four types of chromosomes which result. (After Babcock and Clausen.)

In the diagram *C* and *W* are located in the same chromosome of one parent and *c* and *w* in homologous loci of a similar chromosome of the other parent. If there were perfect linkage, the only gametes produced would be *CW* and *cw*. Owing to a cross-over, however, *Cw* and *cW* are also obtained although less frequently than the combinations *CW* and *cw*. The following outline expresses the result on a percentage basis:

CW 38.7 per cent; *cw* 38.7 per cent

non-cross-over gametes

cW 11.3 per cent; *Cw* 11.3 per cent

cross-over gametes

Accepting the view that factors are located in particular places in the chromosome, the value of the cross-over hypothesis in explaining degrees of factor linkage becomes apparent.

Factors located very close together in the chromosome are closely linked. If it were desired to recombine, in one individual, factors located in different members of a chromosome pair which were in near-by loci, it would be necessary to grow large numbers of individuals and the difficulty of obtaining the desired combination of factors would be very great. Crossing over, however, allows recombinations of factors which are located in the same chromosome pair. This is of great importance as, theoretically, any particular combination of factors can be obtained unless both factors are located in similar loci of homologous chromosomes of related races.

Multiple Allelomorphs.—Certain character expressions are a result of factors located in similar loci of homologous chromosomes. There are, for example, a group of pericarp and cob colors in maize which are a result of multiple allelomorphs. These may be illustrated by citing several examples, although the list is really much greater than that given here (Anderson, 1924). The following homozygous types are known:

- Variety 1, red pericarp, red cob.
- Variety 2, red pericarp, white cob.
- Variety 3, white pericarp, red cob.
- Variety 4, white pericarp, white cob.

If varieties 1 and 4 are crossed, the F_1 resembles variety 1 and in F_2 there are on the average three individuals like variety 1 to one of variety 4. In a cross between 2 and 3, the F_1 resembles variety 1 and in F_2 the parents and F_1 types are obtained in a ratio of one like either parent to two of the F_1 type. In a cross of 1 and 2, the F_1 type is like variety 1 and a 3:1 ratio is obtained in F_2 . These results are best explained by a system of multiple allelomorphs, *i.e.*, characters which are dependent upon factors located in similar loci of homologous chromosomes. All that can be obtained in F_2 from such crosses is in each case the parents and F_1 type. It is theoretically impossible to differentiate multiple allelomorphs and complete linkage. Results similar to those given above could be obtained, if factors for pericarp and cob color were completely linked.

Inheritance of Quantitative Characters.—Many of the important characters of economic plants are size or quantitative characters, such as height of plants, size of seed, or relative date of maturity. It was at first thought that these characters did not follow Mendel's law. The discovery that color characters were frequently due to the interaction of several inherited factors led to the explanation of the inheritance of size characters by similar means. Numerous controlled crosses have been

studied. The general nature of the results in this field may be illustrated by a cross between barley varieties which differ in the average length of internodes of the rachis (see Table I).

In this cross between Hanna and Zeocriton, lax and dense varieties, respectively, the F_2 ranged from above the modal class of Hanna to the modal class of Zeocriton even though only 141 individuals were studied. The calculated coefficient of variability for the F_2 was three or four times greater than for the parental varieties. Several small F_3 families were grown from F_2 plants representing different densities. By examining the table, it will be noted that some F_3 lines bred comparatively true, the tanges for density being no greater than for the parental lines and the

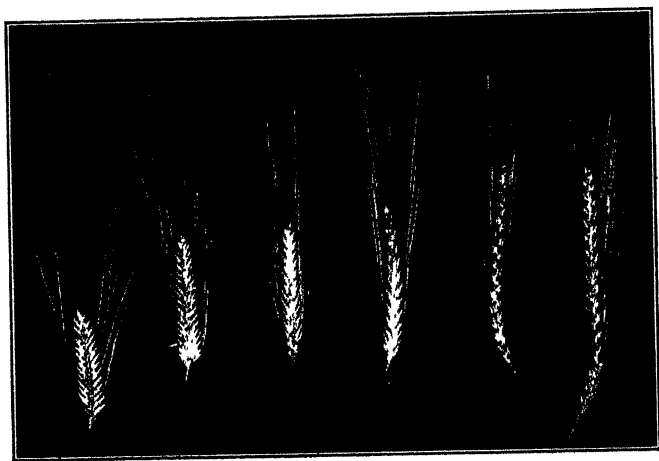


FIG. 9.—Average spikes of the Zeocriton (left), Hanna (right), and four homozygous lines. Mean densities are as follows: Zeocriton, 1.9 millimeters; Hanna \times Zeocriton, 448-1, 2.3 millimeters; 448-5, 2.9 millimeters, 448-11-3, 3.7 millimeters; 448-16, 4.3 millimeters; Hanna, 4.6 millimeters.

coefficients of variability also being low. Other F_3 lines were as variable as the F_2 generation while still others were more variable than the parents but less variable than the F_2 .

Several F_3 lines, which appeared homozygous, were tested in F_4 and some of these on the basis of the more extensive test again, gave evidence of homozygosity. The general nature of the results is illustrated in Fig. 10. These results show that homozygous lines for density may be obtained in F_3 and F_4 , and that in this cross homozygous lines were obtained which approached the densities of the parents as well as homozygous lines with intermediate densities. The determination of just how many factors were involved could not be made without a more extensive test. The results can be explained on a genetic basis by the hypothesis that Zeocriton contains three independently inherited factors for density and that Hanna lacks these factors. The added hypothesis may be

made that each factor in a heterozygous condition gives half as great an effect as when homozygous. The factors may be considered to have a cumulative effect, two factors when present in a homozygous condition producing twice as great an effect as when a single factor is homozygous.

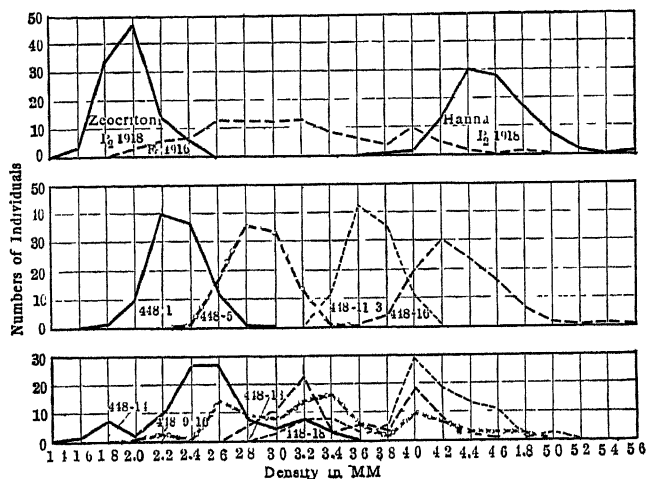


FIG. 10.—Diagrams showing the densities of parental forms and of the F_2 generation in a cross between the Zeocriton and Hanna baileys (upper), of four pure lines (middle), and of several heterozygous lines (lower). (After Hayes and Harlan, 1920)

Other factors of a smaller value are also doubtless present which modify the expression of the main density factors. East and Jones have summarized the results of such controlled crosses and they find a number of general conditions fulfilled.

1 When pure or homozygous races are crossed, the F_1 populations are similar to the parental races in uniformity. This conclusion devolves from observations that if any particular factors AA and aa are homozygous in the parental races, they can only form Aa individuals in the F_1 generation.

2. If the parental races are pure, F_2 populations are similar, no matter what F_1 individuals produce them, since all variability in the F_1 generation is the result of varying external conditions.

3. The variability of the F_2 populations produced from such crosses should be much greater than that of the F_1 populations, and if a sufficient number of individuals are produced the grandparental types should be recovered. The fulfillment of this condition comes about from the general laws of segregation of factors in F_1 and their recombination in F_2 .

4. In certain cases F_2 individuals should be produced showing a greater or a less extreme development of the character complex than either grandparent. This is merely the result of recombination of modifiers, as was explained above.

5. Individuals of different types from the F_2 generation should produce populations differing in type. The idea on which this statement is based is, of course,

that all F_2 individuals are not alike in their inherited constitution and therefore must breed differently.

6. Individuals either of the same or of different types chosen from the F_2 generation should give F_3 populations differing in the amount of their variability. This conclusion depends on the fact that some individuals in the F_2 generations will be heterozygous for many factors and some heterozygous for only a few factors.

A hypothetical case may be given to show how the factor hypothesis may be used to explain the inheritance of quantitative characters. Given two barley varieties as follows:

Variety 1, average length of internode of rachis 2.0 millimeters.

Variety 2, average length of internode of rachis 3.6 millimeters.

Suppose these varieties differ by two separately inherited factors, A and B , each when homozygous causing a lengthening of the internode by 0.8 millimeters; when heterozygous by 0.4 millimeters,

Variety 1 $aabb$ Gamete ab F_1 Zygote $AaBb$
 Variety 2 $AABB$ Gamete AB

Combinations in F_2 would occur as follows:

F_2 PLANTS	F_2 BREEDING NATURE
1 $AABB$	Would breed true for length of internode of 3.6 millimeters.
2 $AaBB$	Would segregate from 3.6 to 2.8 millimeters.
2 $AABb$	Would segregate from 3.6 to 2.8 millimeters.
4 $AaBb$	Would segregate as F_2 .
1 $Aabb$	Would breed true for length of internode of 2.8 millimeters.
2 $Aabb$	Would segregate from 2.8 to 2.0 millimeters.
1 $aaBB$	Would breed true for length of internode of 2.8 millimeters.
2 $aaBb$	Would segregate from 2.8 to 2.0 millimeters.
1 $aabb$	Would breed true for length of internode of 2.0 millimeters.

Probably few size characters are as simple in their inheritance as this illustration. The factor notation, however, assists in gaining a conception of the mode of transmission of these size characters and there seems to be no good reason for believing that a different mechanism is involved from that involved in the inheritance of color characters. Environmental conditions probably play a larger rôle in the modification of the appearance of size characters than for color characters.

The best proof that quantitative characters are inherited in the same general manner as qualitative characters has been obtained from linkage studies. In these studies size or quantitative characters were correlated with qualitative characters which are dependent upon factor pairs whose linkage relations are known. One such case for resistance to the spot-blotch disease in barley, caused by *Helminthosporium sativum*, has been rather extensively studied in Minnesota (Griffie, 1925). The parent varieties were as follows:

SVANHALS	LION
White hull and pericarp	Black hull and pericarp
Two-rowed	Six-rowed
Rough awn	Smooth awn
Resistant to spot blotch	Susceptible to spot blotch

Each of the character pairs, white *versus* black, two-rowed *versus* six-rowed, and rough *versus* smooth awn, appear dependent upon a single-factor difference and independently inherited, that is, the factors for each of these three character differences are in different chromosome pairs. By considering each pair of characters separately, a definite correlation was found in F_2 (each F_2 plant was tested by growing and examining its F_3 progeny) between each of these character pairs and resistance *versus* susceptibility. Thus more of the white plants than of the black were resistant, more six-rowed than two-rowed, and more rough-awned than smooth-awned. Resistance and susceptibility, however, were not dependent upon the same factors which conditioned the other characters, for it was possible to obtain a resistant, white-hulled, two-rowed, smooth-awned variety, and also resistant, black and resistant, six-rowed varieties. It seems fair to conclude that at least three pairs or groups of factors are involved in resistance or susceptibility to *H. sativum* and that these factors are located in the same chromosomes as the factors for color, row number, and smooth *versus* rough awns.

Lethal Factors.—A lethal factor may not necessarily be any different in its inheritance from any other factor. Familiar examples for the plant breeder are chlorophyll-deficient, seedling lethals which cause the death of the seedling after the food supply of the seed is exhausted. Such undesirable factors frequently are observed in plant and animal material and may be thought of as deviations from the normal. By means of such lethals or semilethals which weaken the organism, some idea may be gained of the great complexity of many important normal characters from the inheritance standpoint. Thus deviations from the normal chlorophyll development have been observed in many-selfed lines of maize, and the location of some of the genetic factors involved have been determined. A large number of different chlorophyll variations have been studied which are dependent upon factors located at different places in the chromosomes. Other lethals and semilethals which cause deviations from the normal have been observed. Much of the work of the plant breeder, with some crops, is directed toward eliminating undesirable lethal or semilethal factors from the organism. The origin of these factors is a matter of great interest. It appears, however, that even though they may recur occasionally, it is desirable to eliminate as many of them as possible. Some breeders have held that, since yields were not being rapidly increased by breeding, little could be expected from this mode of attack. With the increased complexity of modern

methods of living, plant diseases and insect pests are rapidly increasing and new diseases are brought in from other regions. The geneticist can do much to aid in keeping our economic plants and animals in their present state of high productivity, as well as help in obtaining higher productivity through controlling the factors of inheritance.

Mutations.—Mutations may be classified as (1) factor mutations and (2) chromosomal aberrations. The lethal factors discussed previously are without doubt examples of changes from the normal dominant condition to the recessive state.

The frequency and nature of factor mutations is a subject of much interest. That changes in factors do occur is rather generally recognized. Stadler (1926) has made a study of the frequency of factor changes for some normal endosperm characters of corn. The method used eliminates contamination as a source of error and permits the determination of the frequency of mutation in the female germ tract previous to megasporogenesis. The following brief description was taken from Stadler:

Suppose we wish to determine the rate of mutation in the gene *C* which in the presence of certain other dominant genes determines aleurone color. When *C* is dominant the aleurone is colored, when *c* is recessive it is colorless. Plants homozygous for the dominant *C* are pollinated by plants homozygous for the recessive.

The heterozygous grains are colored but occasionally a colorless seed is obtained. By growing these colorless grains, Stadler determined that they were genetically colorless and not the result of a non-heritable variation.

The plants produced by the colorless grains were backcrossed to the homozygous recessive *cc* and as colorless seeds were obtained, it appears that the seed planted was homozygous for the recessive condition for the factor *c*. Other tests were conducted which made it seem fairly conclusive that the changes observed were gene mutations, although Stadler stated that "no method will distinguish between a gene mutation and the loss of a section of chromosome too short to reach the next known gene."

The following results were obtained; 6 mutations for *c* in 55,618 chances, 2 mutations for *sh* in 93,106 trials, and no mutations for *wx*, *pr*, or *su* in approximately 12,000 grains each. Apparently, factor mutations are relatively infrequent in maize. The view of factor stability which seems most helpful for the plant breeder has been clearly stated by East and Jones (1919):

For these and other reasons which might be given, could further space be devoted to the subject, we believe there should be no hesitation in identifying the hypothetical factor unit with the physical unit factor of the germ cells. Occasional changes in the constitution of those factors, changes which may have great

or small effects on the characters of the organism, do occur; but their frequency is not such as to make necessary any change in our theory of the factor as a permanent entity. In this conception biology is on a par with chemistry, for the practical usefulness of the conception of stability in the atom is not affected by the knowledge that the atoms of at least one element, radium, are breaking down rapidly enough to make measurement of the process possible.

Chromosomal Aberrations.—The number of chromosomes is specific for each organism and the individuality of each chromosome is an accepted fact by most geneticists. Besides those mutations which consist of changes in a single genetic factor, it is apparent that any change in the chromosome condition is of interest. Chromosomal aberrations may be classified under three general headings: (1) loss or gain of a part of a chromosome called deficiency or duplication; (2) loss or gain of a whole chromosome as a result of non-disjunction; (3) polyploidy, or increase of chromosome numbers as a multiple of a fundamental number.

The chromosomal aberrations classed under the heading of (2) and (3) have been so far the chief sorts which have been found in plant material. The extensive studies of Blakeslee and his coworkers with *Datura* as well as the studies with *Oenothera* prove conclusively that non-disjunction is a cause of various sudden changes which have been observed. Primary non-disjunction occurs when both members of a chromosome pair fail to disjoin and pass to the same pole. This may occur at reduction division and leads to the production of an individual with an extra chromosome which frequently is a cause of a change in the character expression. New types as a result of non-disjunction which breed true have not been obtained in experimental material. Miss Mann (1925), however, as a result of careful studies in *Crepis* species has observed relationships which could be well explained by such a hypothesis. Thus *Crepis capillaris* contains three pairs of chromosomes which can be differentiated from each other by measurements of size. *C. bursiflora* contains two pairs which are similar to the large and small chromosomes of two pairs of *capillaris* and two other pairs, each of which is of similar size to the third pair of *capillaris*.

Many cases of apparent polyploidy are of interest to the plant breeder and there is some circumstantial evidence of such origin. Thus in wheat, oats, and barley some species of each genus contain 7, 14 and 21 pairs of chromosomes, respectively, and it is generally believed that species with the higher chromosome numbers arose from those with lower numbers. In wheat the species known as *Triticum vulgare* to which the varieties of greatest economic importance belong contains 21 pairs of chromosomes, while in the barley genus, *Hordeum*, all of the cultivated varieties contain 7 pairs. Doubling of the chromosome number has occurred in experimental material in *Datura*, *Primula*, and in *Oenothera*, and the new forms bred relatively true. The combined genetic and cytologic attack is

helping to clear up many points in heredity that were formerly more or less of a mystery.

Crosses between Related Species with Different Chromosome Numbers.—In discussions of breeding certain crops, notably wheat, a resumé will be given of crosses between species which differ in chromosome number. It appears sufficient at this point to classify such crosses on the basis of their cytological behavior (see Sax and Sax, 1924).

1. All chromosomes may fail to pair in F_1 . Such results were obtained in a cross between *Crepis setosa* (4 haploid) \times *C. capillaris* (3 haploid). In F_1 plants seven chromosomes were observed. The F_1 plants were partially sterile and reduction division was irregular (Collins and Mann, 1923).

2. A varying number of chromosomes may pair in the F_1 reduction division. Such results were observed by Farmer and Digby in a cross of two species of *Polypodium*.

3. The chromosomes of one parent may pair in F_1 reduction division with some of the chromosomes of the other parent. Such results were observed by Kihara (1919) and Sax (1922) in wheat crosses where the parent species contained 14 and 21 chromosome pairs, respectively.

4. The chromosomes contributed by one parent may not pair with those of the other, but pairing may occur among the chromosomes contributed by only one of the parents. These results were obtained in a cross of *Crepis setosa* (haploid = 4) \times *C. biennis* (haploid = 20). Collins and Mann (1923) thought that the twenty biennis chromosomes paired with each other and that the setosa chromosomes remained unpaired. If such was the case probably biennis is a polyploid species.

5. At reduction division, chromosomes unite in sets of more than two. Thus in triploid *Datura*s the chromosomes are grouped in 12 sets of three chromosomes each at the heterotypic stage of reduction division. Two members of each set pass to one pole and the other member passes to the opposite pole and apparently this occurs at random (Belling and Blakeslee, 1923).

This brief discussion is perhaps sufficient to give some idea of the various types of behavior which may be expected in crosses between related species. For any particular crop where such species crosses are of value, it is necessary to make intensive correlated genetic and cytologic studies. It is probable that some of the peculiar results which have been obtained may be explained eventually by cytological irregularities or by chromosome affinities different in the hybrids than in the parental varieties.

CHAPTER III

BIOMETRICAL METHODS

The use of statistical methods in an analysis of the mode of inheritance of characters, in studies of the correlation between characters and in studies of genetic linkages, together with the need of biometry in an interpretation of the experimental results from field-plot trials, are some of the reasons why the plant breeder should have a working knowledge of biometrical methods. There is considerable variation between separate determinations of such characters as yielding ability, reaction to pathogenic organisms, strength of straw or the feeding value of different crops, and of strains within crop varieties. In some cases, results of a single trial are published and advice is based upon such results.

The purpose of the present chapter is to present some of the more important biometrical tools and to illustrate their mode of calculation and their meaning. It is impossible to treat thoroughly the subject of biometry in a single chapter. Courses in biometry are now given in many of the colleges and universities. The present chapter will serve, perhaps, to help those students who have not had an opportunity to study biometry under a well-trained biometrician. It will also serve as a reference where the more commonly needed biometrical formulæ can be found, together with an illustration of their mode of calculation.

In dealing with such quantitative characters as length of ear in corn or height of plant, numerous measurements will commonly be taken. Because of the work involved, the number of measurements will be limited. By statistical treatment, the results can be analyzed. It is of importance that the sample used for the measurements represent a random sample of the population and that the data be taken accurately. The units of measurement to be used will depend upon the extent of variability of the character which is being studied and upon the degree of precision required.

Constants of the Normal Curve.—The constants most commonly in use are based upon functions of the normal curve of probability or of error, as it is sometimes called. Such a curve is obtained approximately by expanding the binomial $(a + b)^n$ where $a = b = 1$ and n approaches infinity. Polygons representing the expansion of $(a + b)^5$ and $(a + b)^{10}$ are compared with the normal curve (see Fig. 11).

The more important constants are the mean, mode, standard deviation, coefficient of variability, and probable error.

There are various methods of calculation of these constants. The methods illustrated here are, in general, adapted for machine calculation and are those which are recommended by Dr. J. Arthur Harris, who has done much to stimulate the use of biometry as an aid in correct analysis of biological problems.

The mean M is the arithmetical average and is the best measure of type. $M = \frac{\Sigma X}{n}$ where ΣX = sum of the variates and n = total variates.

Where measurements are placed in classes, $X = fV$; where, f = frequency; and V = class center.

The mode is the class of greatest frequency. In a normal curve the mean and mode coincide. In some cases multimodal curves are obtained. In the illustration on page 30 for length of internode of the barley rachis some multimodal curves representing F_3 generations are shown in the lower figure. In these curves the results are due to a combination of environmental conditions together with genetic factors for length of internode.

The standard deviation is an absolute measure of variability in terms of the unit of measurement.

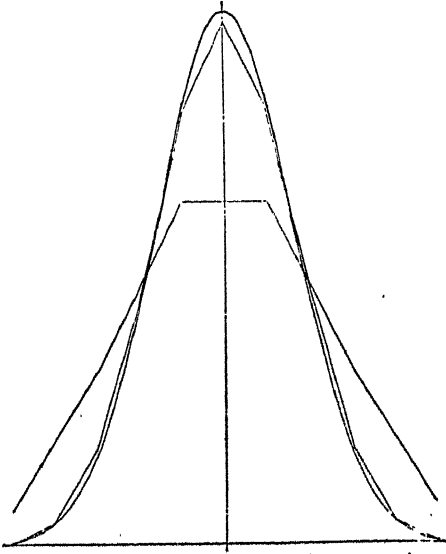


FIG. 11.—Polygons representing expansion of the binomials $(a+b)^5$ and $(a+b)^{10}$ as compared with the normal curve. (After Babcock and Clausen.)

$$\text{S. D.} = \sqrt{\frac{\Sigma(X^2)}{n} - \left[\frac{\Sigma(X)}{n}\right]^2}$$

In a formula frequently given $\text{S. D.} = \sqrt{\frac{\Sigma(f d^2)}{n}}$, where d = deviation of a class from the mean, f = frequency, and n = number of individuals. $n - 1$ is recommended in place of n where the number of individuals is less than 50.

Coefficient of variability is a relative measure of variability in percentage. It is of value in comparing the variability of populations with different means or differing in units of measurement.

$$\text{C. V.} = \frac{\text{S. D.} \times 100}{M}$$

The reliability of a particular biometrical constant is determined by its probable error. The smaller the probable error in relation to the

magnitude of the constant, the greater the confidence that may be placed in the meaning of the constant. The probable error is the quantity, which, when added to and subtracted from the biometrical constant, gives respectively a sum and a difference between which, the chances are even, the true value lies. For example, if the mean height of a certain group of 100 students was 5.7 feet with a probable error of ± 0.1 , the chances are 50:50 that the mean height of another group of 100 students taken from the same population would fall between the limits 5.6 and 5.8 feet. It is apparent, therefore, that the chances are also 1:1 that the mean height would fall outside of the limits set up by 5.6 feet as the lower limit and 5.8 feet as the upper limit.

$$\text{P. E. of a single determination} = \text{S. D.} \times \pm 0.6745.$$

$$\text{P. E. of mean or of } n \text{ determinations} = \frac{\pm 0.6745 \text{ S. D.}}{\sqrt{n}}.$$

$$\text{P. E. of S. D.} = \frac{\pm 0.6745 \text{ S. D.}}{\sqrt{2n}}.$$

$$\text{P. E. of C. V. for a C. V. value of 10 or less} = \frac{\pm 0.6745 \text{ C. V.}}{\sqrt{2n}}.$$

$$\text{P. E. of C. V. for a C. V. value of more than 10} = \pm 0.6745 \frac{\text{C. V.}}{\sqrt{2n}} \left[1 + 2 \left(\frac{\text{C. V.}}{100} \right)^2 \right]^{\frac{1}{4}}.$$

$$\text{P. E. of a difference} = \sqrt{a^2 + b^2 - 2r_{ab} \times a \times b}$$

where a and b represent the probable errors of the separate values being compared and r is the correlation between separate measurements of the quantities being compared. When r is 0, the formula becomes $\sqrt{a^2 + b^2}$

$$\text{P. E. of an average of averages} = \frac{1}{N} \sqrt{a^2 + b^2 + c^2 + \dots + n^2}$$

where N = the number of separate averages and $a \cdot b \cdot c \dots n$ represent the separate probable errors.

For averages representing different numbers for the separate calculations this formula becomes

$$\text{P. E.} = \frac{1}{N} \sqrt{n_1^2 e_1^2 + n_2^2 e_2^2 + \dots + n_n^2 e_n^2}$$

in which n_1, n_2 , etc. are the total numbers within a group; e_1, e_2 , etc. separate probable errors, and N the total numbers in all groups.

The probable error of a Mendelian ratio for numbers may be obtained from the formula $0.6745 \sqrt{pq/n}$ and for percentages from the formula $0.6745 \sqrt{\frac{pq}{n}}$ in which n is the total number of individuals and p and q are the percentages corresponding to the ratios concerned, as 0.75 and 0.25 for a 3:1 ratio (providing neither p or q are very small). Tables of

probable errors of Mendelian ratios have been computed and can be purchased from the Department of Plant Breeding, Cornell University.

In some cases, it is desirable to calculate a mean and standard deviation based upon a small number of individuals. It is generally conceded that at least 20 records should be available, although under certain conditions, computation based upon smaller numbers may be worth while. Definite rules cannot be laid down regarding this or other biometrical problems. In general, provided the work is carried on accurately, a positive relation between numbers and reliability exists. With small numbers of individuals, it is not necessary to place the results in a frequency table.

One of the methods of obtaining an idea of the variability of yields and of the consequent probable error in field-plot trials is to use the results obtained from systematically distributed check plots of a standard variety for the computation. In the following illustration each yield given in bushels represents the average from four systematically distributed rod-row plots of Marquis wheat:

X	X^2
26.9	723.61
24.7	610.09
27.4	750.76
29.3	858.49
24.4	595.36
27.1	734.41
27.8	772.84
24.6	605.16
25.4	645.16
30.3	918.09
27.0	729.00
28.8	829.44
27.9	778.41
25.6	655.36
26.9	723.61
26.6	707.56
<hr/>	
$\Sigma(X)$ 430.7	$\Sigma(X)^2$ 11,637.35

$$\text{Mean of } X = \bar{X} = 430.7 \div 16 = 26.92 \quad \Sigma(X)^2/n = 727.3344.$$

$$\text{S. D.} = \sqrt{727.3344 - 724.6864} = \sqrt{2.6480} = 1.63^1.$$

$$\bullet \quad \text{P. E. of a single determination} = 1.63 \times 0.6745 = 1.10.$$

$$\text{P. E. of mean} = \pm 0.6745 \frac{1.63}{\sqrt{16}} = 0.27.$$

$$\text{P. E. of S. D.} = \pm 0.6745 \frac{1.63}{\sqrt{32}} = 0.19.$$

¹ For small numbers, on the basis of $n - 1$, in the denominator, the calculated value may be multiplied by $\sqrt{\frac{n}{n-1}}$, or $\sqrt{\frac{16}{15}}$.

When larger numbers are available, the separate results are collected in the form of a frequency distribution. If the difference between consecutive class centers is an odd number, it facilitates somewhat the making of the summary and allows the class centers to be whole numbers. In the following frequency distribution, diameters of pollen grains of the varieties of wheat, Marquis, *Triticum vulgare*, and Mindum, *T. durum*, are summarized. The data were taken at Minnesota by Griffec. Class center 57, for example, contains all diameters from 55.5 to 58.4, etc.

TABLE II.—FREQUENCY DISTRIBUTION FOR DIAMETERS OF POLLEN GRAINS OF MARQUIS AND MINDUM WHEATS

Variety	Classes for diameter of pollen grains in microns										Total	Mean	S. D.	C. V.
	42	45	48	51	54	57	60	63	66	69				
Marquis						8	28	45	18	1	100	62.28 ± 0.18	2.62 ± 0.12	4.21 ± 0.20
Mindum	1	1	7	37	32	14	8				100	53.16 ± 0.23	3.40 ± 0.16	6.40 ± 0.31

An illustration of the calculations of the mean and standard deviation for diameters of pollen grains in Marquis wheat is given:

CLASS CENTER V	FREQUENCY f	$\Sigma(X) = \Sigma(fV)$	$\Sigma(X^2) = \Sigma(V^2 \times f)$
57	8	456	25,992
60	28	1,680	100,800
63	45	2,835	178,605
66	18	1,188	78,408
69	1	69	4,761
	<hr/> 100	<hr/> 6,228	<hr/> 388,566

$$M = \frac{6,228}{100} = 62.28.$$

$$S. D. = \sqrt{\frac{388,566}{100} - (62.28)^2} = 6.8616 = 2.62.$$

In actual practice, with machine calculation, only the totals, and not the values of separate calculations, would be carried out.

For the student who does not have available a calculating machine, the short method of computation known as the guess method may be desirable. This method may be found in various textbooks¹ where statistical constants are discussed.

In determining the importance statistically of any calculated result, the probable error is used. A difference between two results, which is 5 to 10 times the probable error of the difference, is sufficiently great so that the chances that the difference is not due to errors of random sampling are very great.

¹ See SINNOTT and DUNN, "Principles of Genetics," p. 245, McGraw-Hill Book Company, Inc., New York, 1925.

The meaning of the probable error can be understood best from a study of a normal curve.

In Germany and some other European countries the standard deviation, sometimes called the standard error, is used in place of the probable error in which case the significance of a result is determined on probability tables based upon the standard deviation. In America probable error is used as the measure of the mathematical significance of the calculated constant providing that controllable errors have been eliminated. Two illustrations may help to make the meaning clear. Suppose the difference between two biometrical constants is 5 and the probable error of the difference is ± 5 . The question arises whether this difference has any significance. In this case the deviation divided by the probable error is

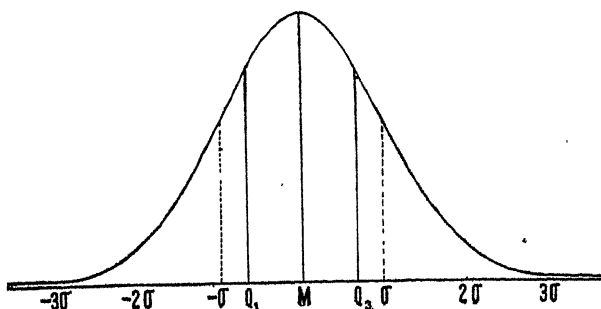


FIG. 12.—A normal curve of error showing the relationship between the quartile, *i.e.*, the probable error of a single variate, and the standard deviation. $Q = 0.6745\sigma$. In this curve the mode, median, and mean are identical. The quartile equals the probable error of a single variate. The proportions of variates within certain areas of the curve are as follows:

within $M \pm Q$, 50 per cent of the variates, within $M \pm \sigma$, 68.3 per cent of the variates; within $M \pm 2Q$, 82.3 per cent of the variates, within $M \pm 2\sigma$, 95.5 per cent of the variates; within $M \pm 3Q$, 95.7 per cent of the variates, within $M \pm 3\sigma$, 99.7 per cent of the variates. (After Babcock and Clausen.)

1 and, therefore, in another similar experiment the probability of the occurrence of a deviation as great or greater than 5 due purely to chance is 50:50 and similarly the odds against the occurrence of a deviation as great as or greater than 5 due to chance is 1:1. In other words the difference 5 ± 5 has no statistical significance but may be attributed wholly to random fluctuation. Suppose, on the other hand, a difference of 10 ± 2 is considered. In this case, the difference divided by its probable error is 5. Opposite the number 5 in the first column of Table III, the number 0.074 is recorded in the second column. This means that in another similar experiment the probability of obtaining a difference as great as or greater than 10 due solely to chance is only 0.074 to 99.926, or stated in another way the odds against the occurrence of a difference as great as or greater than 10 due solely to random fluctuation is 1,350.35 : 1 (third column). Here then is a *real* difference and it becomes necessary to seek a cause for it other than chance fluctuation.

TABLE III.—PROBABILITY OF OCCURRENCE OF STATISTICAL DEVIATIONS OF DIFFERENT MAGNITUDES RELATIVE TO THE PROBABLE ERROR

Deviation divided by P E	Probable occurrence of a deviation as great as or greater than the designated one	Odds against the occurrence of a deviation as great as or greater than the designated one
1 0	50 00	1 00 1
1 1	45 81	1 18 1
1 2	41 83	1 39 1
1 3	38 06	1 63 1
1 4	34 50	1 90 1
1 5	31 17	2 21 1
1 6	28 05	2 57 1
1 7	25 15	2 98 1
1 8	22 47	3 15 1
1 9	20 00	4 00 1
2 0	17 73	4 64 1
2 1	15 67	5 38 1
2 2	13 78	6 26 1
2 3	12 08	7 28 1
2 4	10 55	8 48 1
2 5	9 18	9 89 1
2 6	7 95	11 58 1
2 7	6 86	13 58 1
2 8	5 90	15 95 1
2 9	5 05	18 80 1
3 0	4 30	22 26 1
3 1	3 65	26 40 1
3 2	3 09	31 36 1
3 3	2 60	37 46 1
3 4	2 18	44 87 1
3 5	1 82	53 05 1
3 6	1 52	64 79 1
3 7	1 26	78 37 1
3 8	1 04	95 15 1
3 9	0 853	116 23 1
4 0	0 698	142 26 1
4 1	0 560	174 75 1
4 2	0 461	215 92 1
4 3	0 373	267 10 1
4 4	0 300	332 33 1
4 5	0 240	415 67 1
4 6	0 192	519 83 1
4 7	0 152	656 89 1
4 8	0 121	825 45 1
4 9	0 095	1,051 63 1
5 0	0 074	1,350 35 1
6 0	0 0052	19,230 00 1
7 0	0 00023	434,782 00 1
8 0	0 00000068	1,470,588,234 00 1

Table III presents computations which assist in determining the mathematical significance of the result on a probable-error basis.

Correlation of Characters.—The previous illustrative problems have referred to the variability of expression of a single character and to the means of interpretation. In actual practice, two or more characters frequently must be worked with at the same time. There are two different classes of associations of interest to the plant breeder: (1) those due to physiological causes and (2) those definitely the result of genetic linkages which result from the fact that the character expressions are dependent upon genetic factors located within the same chromosome. In actual practice, as long as environmental conditions remain the same, the same tendency for physiologic correlation of characters would be expected. In considering genetic association, it is to be expected that the genetic linkage can be broken and, in certain lines, a change from a positive association to a negative one would be expected. The usual method of studying the association of two characters, which is not dependent on a known genetic linkage, is by means of a correlation coefficient. In certain cases, the correlation coefficient is a convenient means of determining the extent to which the character is transmitted under the conditions of the experiment.

The coefficient of correlation r is used as a measure of degree of association. Perfect positive correlation is 1 and perfect negative correlation -1 , while intermediate values denote association of a lesser degree. A convenient working formula is

$$r_{xy} = \frac{\Sigma(XY)/n - \bar{X}\bar{Y}}{\sqrt{\Sigma(X^2)/n - [\Sigma(X)/n]^2} \sqrt{\Sigma(Y^2)/n - [\Sigma(Y)/n]^2}}$$

where \bar{X} and \bar{Y} are the means of X and Y , respectively.

If only small numbers of individuals are available for the measurement of each character, the results need not be placed in classes or even in a table. The following illustration is given for this calculation where protein content and loaf volume are the characters studied. The separate strains of wheat were grown at four stations in Minnesota, and the seed for the milling and baking trials was a mixture of equal quantities of seed for each of the four tests. The milling and baking studies were made under the direction of Dr. C. H. Bailey of the Department of Biochemistry of the Minnesota Agricultural Experiment Station.

In the problem, the respective values of X , or loaf volume, and Y , or protein content, are arranged in parallel columns. The means of X and Y are obtained directly by adding the totals for each column and dividing by the number of tests. $\Sigma(X)^2$ and $\Sigma(Y)^2$ are the squared values for each separate entry of X and Y , respectively, and the summation of the same, while $\Sigma(XY)$ = the summation of the product of each value of X by the corresponding value of Y . The problem is illustrated here.

X = LOAF VOLUME	Y = PROTEIN CONTENT	X^2	Y^2	XY
1,080	14.9			
2,030	14.3			
2,235	17.1			
2,245	15.4			
2,285	15.3			
2,225	14.7			
2,030	14.3			
2,070	14.7			
2,010	14.1			
2,000	13.9			
1,990	13.4			
2,010	14.1			
2,060	14.1			
2,000	14.1			
1,930	14.9			
1,970	13.7			
1,980	13.7			
2,010	13.6			
2,020	13.4			
2,010	13.9			
$\Sigma(X) = 41,090$ $\Sigma(X)/n = 2,054.5$	$\Sigma(Y) = 287.6$ $\Sigma(Y)/n = 14.38$	$\Sigma(X)^2 = 84,024,900$ $\Sigma(X)^2/n = 4,231,245$	$\Sigma(Y)^2 = 4,149.96$ $\Sigma(Y)^2/n = 207.198$	$\Sigma(XY) = 592,057.5$ $\Sigma(XY)/n = 29,602.875$

Substituting in the formula for r ,

$$r = \frac{29,602.875 - (2,054.5 \times 14.38)}{\sqrt{4,231,245 - (2,054.5)^2} \sqrt{207.198 - (14.38)^2}} = 0.6910.$$

$$\text{P. E. of } r = \pm 0.6745 \frac{1 - r^2}{\sqrt{n}} = \pm 0.0788.$$

Since $\frac{r}{\text{P. E. } r}$ is 8.8 these data prove very conclusively that there was a direct correlation in this material between protein content and actual loaf volume as determined by a baking trial.

With a larger number of individuals, the data for each character may be placed in classes and the material entered in the form of a correlation table or correlation surface. An illustration is given for the relation between protein content and the number of seeds per ear in corn. The actual class values for number of seeds ranged from 25 to 375, while the class centers were separated by 50 seeds. The class values for protein content ranged from 12.5 to 18.0 with class centers separated by 0.5. For the calculations, arbitrarily selected class centers of 1, 2, 3, etc. were used.

In this problem μX equals the frequency of each class value of X multiplied by the class value of Y and the summation of the same. For example, the calculation of μX for protein content class center 14.5 or 5 may be illustrated. The calculation is as follows:

$$(1 \times 6) + (1 \times 7) + (1 \times 8) = 21.$$

$(\mu X)^2$ may likewise be illustrated for the same class value as for μX

$$(1 \times 6^2) + (1 \times 7^2) + (1 \times 8^2) = 149.$$

Since the products may be added on the machine as obtained, it is not necessary to calculate and record each separate value in the column $\Sigma(yX^2)$.

$\Sigma(XY)$ may be calculated by multiplying each value of yX by the class value of Y and adding or by using the values of xY and multiplying these by the class value of X and their summation. By calculating $\Sigma(XY)$ in both ways, a check on the accuracy of the calculation is obtained.

TABLE IV.—CORRELATION BETWEEN NUMBER OF SEEDS PER EAR AND PROTEIN CONTENT IN SELFED EARS OF F_1 CROSSES, 13-40-227 \times 13-30-211

		Number of seeds per ear classes								f_y	$\Sigma(yX)$	$\Sigma(yX)^2$	$\Sigma(XY)$	$yX = \Sigma yX/f_y$
		25	75	125	175	225	275	325	375					
		1	2	3	4	5	6	7	8					
Protein content in per cent classes	12.5	1						1		1	7	49	7	7
	13.0	2					1	1		2	13	85	26	6.5
	13.5	3					1		1	2	14	100	42	7
	14.0	4						1		1	7	49	28	7
	14.5	5					1	1	1	3	21	140	105	7
	15.0	6					2	2	1	5	34	234	204	6.8
	15.5	7			1	1	3	2		7	41	247	287	5.8571
	16.0	8		2	2	1	3	7	1	16	94	590	752	5.875
	16.5	9		3	5	2	4	1		15	70	350	630	4.6667
	17.0	10	2	1	2	3	1		1	10	34	146	340	3.4
	17.5	11		1	1	1				3	12	50	132	4
	18.0	12		1						1	3	9	36	3
f_x		2	1	9	12	6	15	17	4	66	350	2,058	2,580	

ΣxY	20
$\Sigma(xY)^2$	200
$\Sigma(XY)$	2,580
$\Sigma(xY)/n$	$\frac{20}{66} = \bar{X} = 5.3030$
$\Sigma(xY)^2/n$	$\frac{200}{66} = 3.0303$
$\Sigma(XY)^2/n$	$\frac{2,580^2}{66} = 99.0909$
$\Sigma(XY)/n$	$\frac{2,580}{66} = 39.2273$

$$\Sigma(yX)/n = \frac{350}{66} = \bar{Y} = 5.3030$$

$$\Sigma(yX)^2/n = \frac{2,058}{66} = 31.1818$$

$$\Sigma(XY)/n = \frac{2,580}{66} = 39.2273$$

$$r_{xy} = \frac{\Sigma(XY)/n - \bar{X}\bar{Y}}{\sqrt{\Sigma(yX)^2/n - (\bar{Y})^2} \sqrt{\Sigma(xY)^2/n - (\bar{X})^2}}$$

$$r_{xy} = \frac{39.2273 - 41.5400}{\sqrt{31.1818 - 28.1218} \sqrt{66.4097 - 61.3606}}$$

$$r_{xy} = \frac{-2.3127}{1.7493 \times 2.2603}$$

$$r_{xy} = -0.5849$$

$$P. E. = \frac{0.0745(1 - r^2)}{\sqrt{n}} = 0.0546$$

Regression of X on Y , to be discussed later, $X = (\bar{X} + r_{xy} \frac{\sigma_X}{\sigma_Y} Y) - (r_{xy} \frac{\sigma_X}{\sigma_Y} \bar{Y})$

$$X = 5.3030 + (0.5849 \times \frac{1.7493}{2.2603} \times 7.8333) - (0.5849 \times \frac{1.7493}{2.2603} \bar{Y})$$

$$X = 8.8491 - 0.4527Y$$

The value of a correlation coefficient is determined in relation to its probable error as for any other biometrical constant.

Regression.—Every simple correlation surface has two regressions, *i.e.*, the regressions of X on Y and Y on X . The regression of X on Y is essentially the means of the x -arrays (horizontal) connected by a fitted

curve and similarly the regression of Y on X is the means of the y -arrays (vertical) connected by a fitted curve. If the fitted curve is sensibly a straight line, regression is linear. If regression is linear, the correlation coefficient r is usually used to express the degree of correlation and, if regression is curvilinear, the correlation ratio η is used.

Linearity of regression may be estimated by comparing the broken lines which connect the means of the x - or y -arrays with the plotted straight lines derived from the respective regression equations, but, in most cases, it is safer to rely on more precise methods. The formula for the calculation of the regression of X on Y is as follows.

$$X = \left\{ \bar{X} - r_{xy} \frac{\sigma X}{\sigma Y} \bar{Y} \right\} + \left\{ r_{xy} \frac{\sigma X}{\sigma Y} Y \right\}.$$

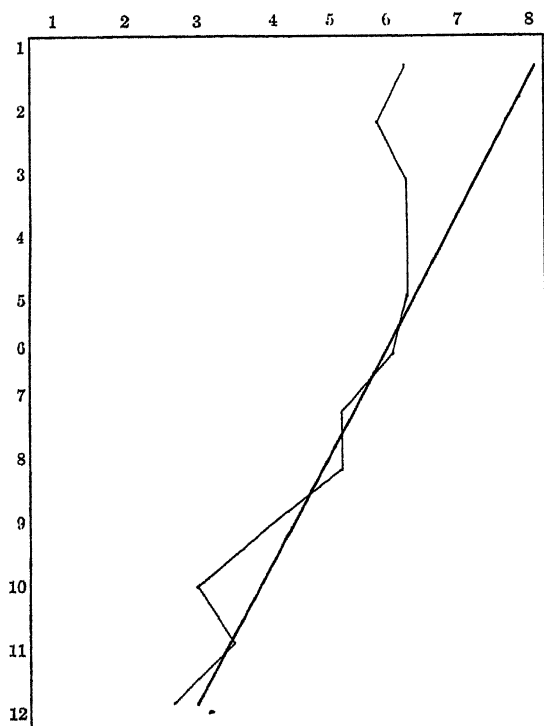


FIG. 13.—Regression of number of seeds per ear on protein content.

In substituting in this formula, it is necessary to use the sign of the correlation coefficient in the usual algebraic manner. For a correlation coefficient of -0.5 , the quantity $-r_{xy}$ becomes $+0.5$.

An illustration of a graphical test for linearity of regression of X on Y will be given. First, it is necessary to obtain the means of the various

x -arrays (rows). For example, in Table IV, ${}_y\bar{X} = \Sigma_y X / f_y$, *i.e.*, the mean of each horizontal frequency distribution is calculated and entered in the last column at the right of the Table. These means are plotted (broken line) in Fig. 13.

The next step is to calculate the regression of X on Y or, in other words, the regression of number of seeds per ear on protein content. By substituting the proper values in the formula given above, the equation becomes $X = 8.8491 - 0.4527Y$. In this equation X is the dependent variable and Y is the independent one or, in other words, the value of X is determined by the particular value which is assigned to Y . To plot the straight line represented by the equation, it is necessary to determine two values of X only. Let the values of the end classes of Y , or 1 and 12, be substituted in the equation.

$$X = 8.8491 - 0.4527 \times 1, \text{ or } 8.3964.$$

$$X = 8.8491 - 0.4527 \times 12, \text{ or } 3.4167.$$

By connecting the two points ($X = 8.8491$, $Y = 1$ and $X = 3.4167$, $Y = 12$), the desired straight-line regression of X on Y , shown in Fig. 13, is obtained.

In general, the regression appears approximately linear when it is noted that there are small frequencies in the classes for low protein content. This gives a graphical test of linearity.

The student may have observed from the illustration just given that the regression equation is useful for predicting values. For example, in the problem at hand it is possible to estimate the number of seeds per ear from the protein content and, similarly, by means of the regression equation of Y on X , it is possible to estimate the protein content from the number of seeds per ear. The greater the correlation between two sets of variables, the more accurately may the value of one variable be predicted from a known value of the other.

The Correlation Ratio.—The second (and a truly mathematical) measure of linearity of regression is obtained by comparing the correlation coefficient with the correlation ratio. The correlation ratio is of value, also, where one of the variables is measured in categories such as color of glume in small grains and the other in numerical values. Its calculation is given here. The formula for the correlation ratio is as follows:

$$\eta_{xy} = \sqrt{\frac{\sum f_y (\bar{X}_y - \bar{X})^2 / n}{\sigma_X^2}}$$

The calculations are as follows: Where ${}_y\bar{X}$ = mean of values of X for each class of Y ; \bar{X} = mean of X . The data for protein content and number of seeds can be used in the illustration.

fy	${}_y\bar{X}$	${}_y\bar{X} - \bar{X}$	$({}_y\bar{X} - \bar{X})^2$	$f{}_y({}_y\bar{X} - \bar{X})^2$
1	7	1 6970	2 8798	2 8798
2	6 5	1 1970	1 4328	
2	7	1 6970	2 8798	
1	7	1 6970	2 8798	
3	7	1 6970	2 8798	2 2410
5	6 8	1 4970	2 2410	
7	5 8571	0 5541	0 3070	
16	5 875	0 5720	0 3272	
15	4 6667	0 6363	0 4049	3 6214
10	3 4	1 9030	3 6214	
3	4	1 3030	1 6978	
1	3	2 3030	5 3038	
66	_____	_____	_____	94 2981

$$\sqrt{\frac{\sum [f{}_y({}_y\bar{X} - \bar{X})^2]}{n}} = \sqrt{\frac{942981}{66}} = \sqrt{142875909} = 1.1953$$

$$\eta = \frac{1.1953}{1.7493} = 0.6832$$

In the following comparison Blakeman's test for linearity is used. The formula is stated in terms of the probable error of the difference between η^2 and r^2 . It is taken from Pearl's "Medical Biometry and Statistics," and is as follows:

$$\text{P. E. } \eta^2 - r^2 = 2 \times \frac{0.67449}{\sqrt{n}} \times \sqrt{\eta^2 - r^2} \times \sqrt{(1 - \eta^2)^2 - (1 - r^2)^2 + 1}.$$

The calculation is given here:

$$\text{P. E. } \eta^2 - r^2 = 2 \times 0.08302 \times \sqrt{(0.6832)^2 - (0.5849)^2} \times \sqrt{(0.533238)^2 - (0.657892)^2 + 1}.$$

Solving, P. E. $\eta^2 - r^2 = 0.0594$

The difference between η^2 and r^2 is 0.1247. The difference is 2.3 times its probable error which is not very significant. It may be concluded that the regression is sensibly linear.

In the illustration of the calculation of the correlation ratio, only 66 individuals were studied. The statement is generally made that η should not be used for small numbers as the outlying individual in the correlation surface has a great effect on the correlation ratio. For the experimental biologist, however, small numbers are frequently a necessity and the value of η is an aid in drawing the best possible conclusions.

In a study of the correlation between varietal yields in relation to some such factor as reaction to a particular disease organism, the data for each individual variety are based as a rule on the results of several replicated plots, and disease reaction is obtained under controlled epidemic conditions. In a correlation in which only 66 entries appear in

the table, each entry is, in many cases, based on several observations under controlled conditions.

The Coefficient of Contingency.—When both series of variables are measured in categories, the coefficient of contingency may be used. Its calculation may be illustrated by a study of the degree of infection of 67 barley varieties or strains by *Helminthosporium sativum*, the spot-blotch disease. In this study the infection degree was studied when the barley was nearly mature. Separate notes were taken on the degree of infection of heads, culms, and roots. The terms "heavy," "medium," "light," and "trace" were used and were modified by the addition of + or - for very heavy and less heavy, respectively. In the table the classes $h+$, h , $h-$, etc., are denoted by A , B , C , etc.

TABLE V.—CORRELATION BETWEEN THE DEGREE OF INFECTION OF 67 BARLEY STRAINS OR VARIETIES FOR 1921 AND 1922

	Degree of infection, 1922										<i>f</i>	Calculation	Chances
	<i>H</i>	<i>I</i>	<i>J</i>	<i>K</i>	<i>L</i>	<i>M</i>	<i>O</i>	<i>P</i>	<i>R</i>				
	<i>H</i> <i>H</i> —	<i>M</i> +	<i>M</i>	<i>M</i> —	<i>L</i> +	<i>L</i>	<i>L</i> —	<i>Tr</i>					
<i>AH</i> +	1		1	1	1						4	$\frac{3}{67}$	0.0597
<i>BH</i>	2	1	1								4	$\frac{3}{67}$	0.0597
<i>CH</i> —	2	1	5	1		3	1				13	$\frac{13}{67}$	0.1940
<i>DM</i> +	1	1	3	1	1	2		5			14	$\frac{14}{67}$	0.2090
<i>EM</i>			1		2	3	2	5	6		19	$\frac{19}{67}$	0.2836
<i>FM</i> —					2	2	3	1	1		9	$\frac{9}{67}$	0.1343
<i>GL</i> +					1	2		1			4	$\frac{3}{67}$	0.0597
	6	3	11	3	7	12	6	12	7				

The calculation of the expected number of individuals in each 1922 class for a total of four, and for class A in 1921, is obtained by dividing 4 by 67, or 0.0597. This is given under the heading of "chances" at the right of the correlation surface. The calculated number for each class in the table was obtained by multiplying the "chances" by the total number of individuals in the group concerned. Thus for a total number in H of 6, the calculated number for AH is 6×0.0597 or 0.3582 and the calculated number for AI is $3 \times 0.0597 = 0.1791$, etc.

X^2 is obtained from the usual formula $X^2 = (O - C)^2 / C$. $\phi^2 = \frac{X^2}{n}$ and the coefficient of mean square contingency $= C' = \sqrt{\frac{\phi^2}{1 + \phi^2}}$.

For rough judgments the Probable Error of the mean square contingency $= P. E. C' = 2 \times 0.6745 \frac{1 - C'^2}{\sqrt{n}}$.

The calculation is illustrated in detail:

O		C	O - C	(O - C) ² /C
AH	1	0 3582	0 6118	1 1499
AI	0	0 1791	0 1791	0 1791
AJ	1	0 6567	0 3433	0 1795
AK	1	0 1791	0 8209	3 7626
AL	1	0 4179	0 5821	0 8108
AM	0	0 7164	0 7164	0 7164
AO	0	0 3582	0 3582	0 3582
AP	0	0 7164	0 7161	0 7164
AR	0	0 4179	0 4179	0 4179
BH	2	0 3582	1 6418	7 5251
BI	1	0 1791	0 8209	3 7626
BJ	1	0 6567	0 3433	0 1795
BK	0	0 1791	0 1791	0 1791
BL	0	0 4179	0 4179	0 4179
BM	0	0 7164	0 7164	0 7164
BO	0	0 3582	0 3582	0 3582
BP	0	0 7164	0 7164	0 7164
BR	0	0 4179	0 4179	0 4179
CH	2	1 1640	0 8300	0 6004
CI	1	0 5820	0 4180	0 3002
CJ	5	2 1340	2 8660	3 8401
CK	1	0 5820	0 4180	0 3002
CL	0	1 3580	1 3580	1 3580
CM	3	2 3280	0 6720	0 1940
CO	1	1 1640	0 1640	0 0231
CP	0	2 3280	2 3280	2 3280
CR	0	1 3580	1 3580	1 3580
DI	1	1 2540	0 2540	0 0514
DJ	1	0 6270	0 3730	0 2219
DK	3	2 2990	0 7010	0 2137
DL	1	0 6270	0 3730	0 2219
DM	1	1 4630	0 4630	0 1465
DO	2	2 5080	0 5080	0 1029
DP	0	1 2540	1 2540	1 2540
DR	5	2 5080	2 4920	2 4761
EH	0	1 4630	1 4630	1 4630
EI	0	1 7016	1 7016	1 7016
EJ	0	0 8508	0 8508	0 8508
EK	1	3 1196	2 1196	1 4402
EL	0	0 8508	0 8508	0 8508
EM	2	1 9852	0 0148	0 0001
EO	3	3 4032	0 4032	0 0478
EP	2	1 7016	0 2984	0 0523
ER	5	3 4032	1 5908	0 7492
FI	6	1 9852	4 0148	8 1194
FH	0	0 8058	0 8058	0 8058
FI	0	0 4029	0 4029	0 4029
FJ	0	1 4773	1 4773	1 4773
FK	0	0 4029	0 4029	0 4029
FL	2	0 9401	1 0599	1 1950
FM	2	1 6116	0 3884	0 0936
FO	3	0 8058	2 1942	5 9748
FP	1	1 6116	0 6116	0 2321
FR	1	0 9401	0 0599	0 0038
GH	0	0 3582	0 3582	0 3582
GI	0	0 1791	0 1791	0 1791
GJ	0	0 6567	0 6567	0 6567
GK	0	0 1791	0 1791	0 1791
GL	1	0 4179	0 5821	0 8108
GM	2	0 7164	1 2836	2 2999
GO	0	0 3582	0 3582	0 3582
GP	1	0 7164	0 2836	0 1123
GR	0	0 4179	0 4179	0 4179
...	68 7989

$$\chi^2 = \frac{\sum (O - C)^2 / C}{n} = \frac{68\ 7989}{87} = 1.0268$$

$$\text{Coefficient of contingency} = \sqrt{\frac{\phi^2}{1 + \phi^2}} = \sqrt{\frac{1.0268}{2.0268}} = \sqrt{0.5066} = 0.7118$$

$$P. E. C' = 2 \times .08240 \times .493341 = .0813.$$

The X^2 Method of Studying "Goodness of Fit."—Because the coefficient of contingency is similar in calculation to the X^2 , its inclusion at this point appears desirable. It is particularly applicable to Mendelian segregation when more than two phenotypic classes are considered. The application of this method to Mendelian results was suggested by Harris (1912). The method is illustrated:

Phenotype	Observed O	Calculated C	$O - C$	$(O - C)^2$	$\frac{(O - C)^2}{C}$
Purple, starchy.....	1,861	1,822.5	38.5	1,482.25	0.81
Purple, sweet.....	614	607.5	6.5	42.25	0.07
White, starchy.....	548	607.5	59.5	3,540.25	5.83
White, sweet.....	217	202.5	14.5	210.25	1.04

$$X^2 = \sum \left[\frac{(O - C)^2}{C} \right] = 7.75$$

For four classes and $X^2 = 7.75$ the value of P may be looked up in the table (see Pearson's tables, 1914). On this basis probability, or $P = 0.0525$. This may be interpreted that a worse result might be expected on the basis of random sampling 525 times in 10,000 trials, or 1 in 19.0 trials.

In one comparison made by G. Udny Yule (1923) a probability of 0.86 was obtained. This was interpreted in his words, "so that we might expect a worse agreement 8 or 9 times in ten trials."

Partial Correlations.—When more than two series of variables have been considered and all possible relationships have been determined, it is frequently desirable to hold constant all factors considered except the two. The true importance of each variable can be determined by this method. In case any one variable does not appear to be related to any of the others by means of simple product-moment coefficients of correlation, this variable should be discarded from the study. In most cases, it will be necessary to calculate first the simple product-moment coefficients.

Studies of loaf volume in wheat in relation to three other variables protein content, a factor representing quality of gluten, and diastatic activity—may be used in illustration. The original data are presented in the following table:

TABLE VI.—1924 MILLING RESULTS

Mixture of Seed from University Farm, Crookston, Morris, and Waseca in Proportion of 2:2:2:1 lb, respectively¹

Chem- istry number	Variety	Loaf volume	Protein H ₂ O	Quality of gluten	Dia- static activity
8,735	Marquis	1,980	14.9	2.4	65
8,736	Marquis × Kota, II-19-9	2,030	14.3	2.5	144
8,737	Kota Natural Cross, II-18-33	2,235	17.1	2.0	105
8,738	Kota Natural Cross, II-18-21.	2,245	15.4	1.9	98
8,739	Kota Natural Cross, II-19-2	2,285	15.3	2.2	100
8,740	Marquis × Kota, N. D. 1656	2,225	14.7	2.5	97
8,741	Marquis × Kota, N. D. 1658	2,030	14.3	2.2	90
8,742	Kota	2,070	14.7	2.7	90
8,743	Marquis	2,010	14.1	2.6	52
8,744	Marquis × Kanred, II-17-4	2,000	13.9	2.0	89
8,745	Marquis × Kanred, II-17-14	1,990	13.4	2.1	69
8,746	Marquis × Kanred, II-17-16.	2,010	14.1	2.5	61
8,747	Marquis × Kanred, II-17-22	2,060	14.1	2.4	71
8,748	Marquis × Kanred, II-17-37	2,000	14.1	2.6	88
8,749	Marquis × Kanred, II-17-40	1,930	14.9	2.3	102
8,750	Marquis × Kanred, II-18-44	1,970	13.7	2.4	119
8,751	Marquis × Kanred, II-18-8	1,980	13.7	2.3	94
8,753	Marquis × Kanred, B2-5	2,010	13.6	2.6	40
8,754	Marquis × Kanred, B8-11	2,020	13.4	2.5	92
8,755	Marquis	2,010	13.9	2.4	64

¹ The data used were furnished by the Department of Agricultural Biochemistry, Minnesota Agricultural Experiment Station, the work being carried out under the direction of Dr. C. H. Bailey.

Spring wheats, grown in 1924, were used in the study. Each strain used in the test belonged to the bread-wheat species, *Triticum vulgare*. In this problem loaf volume = 1, protein content = 2, quality of gluten = 3, and diastatic activity = 4. Calculated-product, moment coefficients are:

	1	2	3
2	0.6910 ± 0.0788		
3	-0.3695 ± 0.1302	-0.4134 ± 0.1251	
4	0.2467 ± 0.1416	0.3081 ± 0.1365	-0.2386 ± 0.1422

At present the normal equation method of obtaining partial correlations is favored. The calculations may proceed from the regression values, the formulæ for partial correlations being as follows where 1, 2, 3, and 4 represent the various series of variables in the study:

$$r_{12.34} = \sqrt{\beta_{12.34}\beta_{21.34}}$$

$$r_{13.24} = \sqrt{\beta_{13.24}\beta_{31.24}}$$

By the method of normal equations the regression values are calculated directly.

The first normal equation may be written as follows: $r_{11} + r_{12} + r_{13} + r_{14} = \text{sum}$. This may be read, the correlation of 1 or loaf volume with itself and with each of the other variables. For this equation the calculated regression coefficients would be $\beta_{41.23}$, $\beta_{42.13}$, and $\beta_{43.21}$. It will be noted that the regressions for any series of variables can be obtained directly without obtaining an intermediate series. Thus $\beta_{43.12}$ is calculated directly without calculating first $\beta_{43.1}$, etc.

The rule for setting up the first normal equation is that the last term of the normal equation is the first term of the regression coefficient and the second term is the term in the same vertical column.

Calculation of reductions to obtain Ia, IIa, IIIa, etc. (see problem, below).

Directions. Step 1.—Bring down actual product-moment coefficients for 1 with other groups = 1. (It will be noted that the correlation of 1 with 1 = 1, or 2 with 2 = 1, etc.) Change signs and enter in a new row = Ia.

Step 2.—Bring down next series of correlation coefficients for 2 with other groups. In obtaining sum of this column, add other correlations in the same vertical column. For example, $0.6910 + 1 - 0.4143 + 0.3081 = 1.5857$. Multiply I by second term of Ia and bring down. Note that no multiplications are considered for the vertical column at left. Add = II. Divide by first term of II and change signs = IIa.

Step 3.—Proceed as for step 2. Bring down next series of correlation coefficients for 3 with other groups. Note that other correlations in the same vertical column are used in obtaining the sum. Thus, $-0.3695 - 0.4134 + 1 - 0.2386 = -0.0215$. Multiply I by third term of Ia and bring down. Multiply II by second term of IIa and bring down. Sum = III. Divide by first term of III and change signs = IIIa.

	1	2	3	4	Sum
I	1	0.6910	-0.3695	0.2467	= 1.5682
Ia	-1	-0.6910	+0.3695	-0.2467	= -1.5682
		1	-0.4134	0.3081	= 1.5857
		-0.4775	+0.2553	-0.1705	= -1.0836
II		0.5225	-0.1581	+0.1376	= 0.5021
IIa		-1	+0.3026	-0.2634	= -0.9610
			1	-0.2386	= -0.0215
			-0.1365	+0.0912	= +0.5794
			-0.0478	+0.0416	= +0.1519
III			0.8157	-0.1058	= +0.7098
IIIa			-1	+0.1297	= -0.8702
			-0.1297		
		0.2242	-0.0392	0.2634	
	0.0439	-0.1549	-0.0479	0.2467	

Calculation of Regressions.—1. Bring down last figure in IIIa at left of = sign. Transfer 1 place to left and change signs = first regression $\beta_{13\ 12} = -0.1297$.

2. Bring down and change signs in IIa and Ia rows at left of = sign. Multiply first regression by values of IIa and Ia in same vertical column and bring down. $-0\ 1297 \times 0.3026 = -0.0392$ and $-0\ 1297 \times 0\ 3695 = -0.0479$. Add horizontal upper line of this step: $0.2634 - 0\ 0392 = 0.2242$, which is the regression of $\beta_{12\ 13}$.

3. Multiply second regression by value of Ia in same vertical column, $0.2242 \times -0.6910 = -0.1549$. Add horizontal line of this step. $0.2467 - 0\ 0479 - 0.1549 = 0.0439$, which is the regression $\beta_{11\ 23}$.

Regression of other variables can be calculated in a similar manner. For example, to obtain regression of 14.23, it will be necessary to start with a normal equation in which loaf volume 1 is at the left of the equals sign, or $r_{22} + r_{23} + r_{24} + r_{21} = \text{sum}$. The calculated regressions $\beta_{11\ 23}$ and $\beta_{14\ 23}$ are, respectively, 0.0439 and 0.0254. Substituting in the formula

$$r_{41\ 23} = \sqrt{\beta_{14\ 23}\beta_{41\ 23}},$$

$$r_{11\ 23} = \sqrt{0.0439 \times 0.0254} = 0.0334$$

The calculated simple and partial correlation coefficients are:

$$r_{12} = 0\ 6910 \pm 0\ 0788$$

$$r_{13} = -0\ 3695 \pm 0\ 1302$$

$$r_{14} = 0\ 2467 \pm 0\ 1416$$

$$r_{23} = -0\ 4134 \pm 0\ 1251$$

$$r_{24} = 0\ 3081 \pm 0\ 1365$$

$$r_{14} = -0\ 2386 \pm 0\ 1422$$

$$r_{12\ 14} = 0\ 6216 \pm 0\ 0925$$

$$r_{13\ 21} = -0\ 1222 \pm 0\ 1486$$

$$r_{14\ 23} = 0\ 0334 \pm 0.1507$$

$$r_{23\ 14} = -0\ 2101 \pm 0\ 1142$$

$$r_{24\ 13} = 0\ 1647 \pm 0.1467$$

$$r_{34\ 12} = -0.1233 \pm 0.1485$$

Multiple Correlations.—The multiple correlation coefficient expresses the degree to which the dependent variable is dependent upon the other factors considered. If the coefficient of multiple correlation is low, it is apparent that some important factor or factors have not been taken into account. In general, the multiple correlation coefficient should be 0.9 or above if all essential factors have been considered.

If the partial correlations have been computed by the normal equation method, the multiple correlation coefficient may be calculated from the simple product moment correlation coefficients and from the partial regression values by the following:¹

$$R^2_{1.234 \dots n} = (\beta_{12\ 34} \dots n r_{12}) + (\beta_{13\ 24} \dots n r_{13}) + (\beta_{14\ 23} \dots n r_{14}) + (\beta_{1n\ 234} \dots n -1 r_{1n})$$

By substituting in this formula the respective values of the partial regression values and of the simple product-moment correlation coefficients and making the necessary calculations, it is possible to determine the

¹ WALLACE and SNEDECOR, "Correlation and Machine Calculation," *Iowa Off. Pub.*, vol. 23, No. 35, p. 34.

extent to which the dependent variable, loaf volume in the wheat study, is a result of the independent variables considered.

Performing the necessary calculations the value of $R_{1.234}$ was found to be 0.6975. A study of the meaning of this value indicates to what extent the factors governing loaf volume have been considered.

An Interpretation of the Meaning of the Correlation Coefficient.—The meaning of correlation coefficients of different magnitude is of primary interest. If the coefficient of correlation is 0.5, it is true that it is half as great as the largest possible coefficient or 1. A relation of +1, however, means that the entire variability of the dependent variable is a result of the variability of the independent variable or that the variability of both dependent and independent variables is a result of the same fundamental cause or causes. The extent to which total variability is a function of the factors considered in computing any particular correlation coefficient can be determined by the appropriate formula. The following computation was taken from Richey's (1924) publication:

TABLE VII.—EXPECTED REDUCTION IN VARIABILITY FOR VARIOUS CORRELATION COEFFICIENTS (*Richey*)

$r =$	Reduction in variability $= 100 \times 1 - \sqrt{1 - r^2}$, per cent	$r =$	Reduction in variability $= 100 \times 1 - \sqrt{1 - r^2}$, per cent
0.4	08.4	0.8	40.0
0.5	13.4	0.866	50.0
0.6	20.0	0.9	56.4
0.707	29.3	1.0	100.0

With a multiple correlation coefficient or big $R_{1.234}$ of 0.6975, substitution can be made in the formula $100(1 - \sqrt{1 - r^2})$ which gives a percentage value of 28.2. Twenty-eight and two-tenths per cent expresses the reduction in variability as expressed by the probable error of the predicted loaf volumes as compared with the variability of the actual loaf volumes taken about their mean.

If it is desired to determine the proportion of variability in the dependent variable which may be attributed to its relation with the independent variables, R^2 , expressed as a percentage figure, should be used. R^2 measures the proportion of total squared variability in the dependent variable which may be explained in terms of its mathematical relations to the independent variables, leaving the amount expressed by $1 - R^2$ yet to be accounted for.

CHAPTER IV

FIELD-PLOT TECHNIC

The field is the plant breeder's laboratory and the question of correct field technique is of the utmost importance.

In carrying out crop-breeding studies, the number of varieties and strains has been greatly multiplied. Vilmorin's isolation principle, whereby the value of any selection is determined by the breeding nature of the progeny, has been universally adopted.

The difficulties of making all conditions of similar nature for a large number of strains or varieties which must be tested are very numerous. The method used must be such that the performance will be a correct indication of the comparative value of the strains when grown under farming conditions. The purpose of the present chapter is to discuss field-plot technic for such disturbing factors as soil heterogeneity and climatic conditions.

SOIL HETEROGENEITY

The field selected for the comparative trials should be representative of the soil and climatic conditions under which the crop will be grown. The land must then be cropped in such a manner that it is kept in a uniform state of good productivity. In order to do this, it is necessary to observe some one of the standard rotations. It is a good practice to have one or more bulk crops rotated with the breeding plots in order to keep the land uniform. If only one area of land is available, there is then no choice and the investigator must see that this field is treated in the best possible way. If more than one field is available, it is possible to determine which is more nearly uniform by a correlation of contiguously grouped plots, as outlined by Harris (1915).

The Universality of Soil Heterogeneity.—Before presenting this and other methods of determining the relative variability in productivity of different fields or different areas of the same field, it may be desirable to gain some idea of the prevalence of soil heterogeneity. The use of the correlation coefficient was suggested as a means of learning the extent of soil variability. This coefficient measures the degree to which near-by plots are similar in productivity and allows a comparison of heterogeneity in different fields and in widely separated localities. Correlation coefficients may range from 0.0 to 1 and may be either positive or negative.

In nearly all studies of heterogeneity, adjacent plots have proved to be somewhat similar in productivity and, as a result of the studies, the universality of soil heterogeneity has been established. Many of these studies have been conducted by Harris (1920), the fields used being representative of the land available for experimental work. As will be illustrated in the problem, the field studied has commonly been grown to one crop and at harvest time yields have been determined from small plots harvested separately. The extent to which contiguous plots resemble each other in yield is determined by the correlation coefficient; the larger the coefficient, the greater the degree of soil heterogeneity.

In the following summary the size of plots harvested, the characters studied, the investigator who furnished the original data, and the correlation coefficients are listed:

TABLE VIII.—CORRELATION COEFFICIENTS PRESENTED BY HARRIS WHICH EXPRESS THE EXTENT OF SOIL HETEROGENEITY IN DIFFERENT LOCALITIES AND WITH DIFFERENT CROPS

Crop	Character	Size of plot	Investigator	Correlation coefficient
Wheat.....	Yield, grain	5.5 by 5.5 feet	Montgomery, Nebr.	0.603 \pm 0.020
Wheat.....	Nitrogen content	5.5 by 5.5 feet	Montgomery, Nebr.	0.115 \pm 0.044
Oats.....	Yield, grain	$\frac{1}{80}$ acre	Kiesselsbach, Nebr.	0.405 \pm 0.035
Mangels.....	Yield, roots	$\frac{1}{200}$ acre	Mereer and Hall, England (Rothamsted)	0.346 \pm 0.042
Mangels.....	Yield, leaves	$\frac{1}{200}$ acre	Mereer and Hall, England (Rothamsted)	0.466 \pm 0.037
Potatoes.....	Yield	Rows, 72 feet, 7 inches long	Lyon	0.311 \pm 0.043
Corn.....	Yield, grain	$\frac{1}{10}$ acre	Smith, Ill. (1895)	0.830 \pm 0.019
Alfalfa.....	Yield, hay			
	1913, first cutting	0.085 acre	Seafield, Huntley Experiment Farm, Mont.	0.407 \pm 0.059
	1913, second cutting	0.085 acre		0.343 \pm 0.062
	1914, first cutting	0.085 acre		0.602 \pm 0.045
	1914, second cutting	0.085 acre		0.657 \pm 0.040

The data presented in Table VIII are only a small part of those available and are furnished for the purpose of emphasizing the usual extent of soil heterogeneity in plot studies.

The physical and chemical bases of the heterogeneity of soil have been studied to some extent. The investigations have been conducted in a similar manner as those previously mentioned. Actual measurement of the factors concerned must be made over the field and the heterogeneity coefficient applied. Moisture content per foot has been investigated at the San Antonio Experimental Farm. The coefficients computed determine the correlations between the percentages of water content of associated plots (see Table IX).

TABLE IX—CORRELATION COEFFICIENTS FOR WATER CONTENT OF THE SOIL OF ASSOCIATED PLOTS

Depth	Correlation
First foot	0 317 \pm 0 065
Second foot	0 529 \pm 0 052
Third foot	0 542 \pm 0 051
Fourth foot	0 704 \pm 0 036
Fifth foot	0 607 \pm 0 045
Sixth foot	0 481 \pm 0 055

It will be noted that there is marked and statistically significant heterogeneity in soil moisture content at six different levels in the upper 6 feet of soil.

Likewise, coefficients of heterogeneity for carbon and nitrogen content were studied in a silty clay loam at Davis and a blow sand at Oakley, Calif. Eighty samples, distributed at 30-foot intervals, were used. The results for the silty clay loam at Davis were:

For carbon, $r = 0.417 \pm 0.063$

For nitrogen, $r = 0.498 \pm 0.057$

For the blow sand at Oakley:

For carbon, $r = 0.317 \pm 0.068$

For nitrogen, $r = 0.230 \pm 0.072$

These and other studies have proved the practical universality of soil heterogeneity. One of the concluding statements made by Harris sums up the present status:

The demonstration that the fields upon which plot tests have been carried out in the past are practically without exception so heterogeneous as to influence profoundly the yields of the plots emphasizes the necessity for greater care in agronomic technic and more extensive use of the statistical method in the analysis of the data of plot trials if they are to be of value in the solution of agricultural problems.

Before presenting some of the methods now available for partially overcoming the harmful effects of soil heterogeneity, the biometrical methods which have been used to express the extent of soil heterogeneity will be outlined.

Harris' Method of Estimating Soil Heterogeneity.—By Harris' method, the coefficient of correlation is used as an index of soil uniformity. This statistical constant measures the degree of correlation between contiguous plots grouped in a certain way. If the variation in yield from plot to plot is simply due to random sampling, there will be no correspondence between contiguously grouped units. On the other hand, if the field is "patchy," certain contiguous units tend to yield high while

others show a tendency in the opposite direction. Under these conditions a high correlation coefficient results. If variability due to random sampling only is entering, the correspondence between some contiguous plots will be counterbalanced by the lack of correspondence between others, providing that the number of ultimate units is sufficiently large to permit an expression of the law of average. It is obvious that in the application of Harris' method the field must receive the same treatment (seed, cultivation, fertilizer, etc.). The division of the field into the desired units may be made at any time before the crop is harvested, but preferably before or soon after planting in order to minimize possible injury to the growing crop.

A simple illustration will make the calculation of the correlation coefficient clear, although a much larger number of units should be used in an actual study of the reliability of a field for plot work. Suppose a certain field is divided into 16 units and these units are in turn arranged in 4 groups. Let p_1, p_2, p_3 etc. represent the ultimate units and C_{p1}, C_{p2} , etc., represent the groups. By assigning values for yield in bushels per acre to the ultimate units, one may make the calculation necessary to apply the formula. The value of any particular group is the sum of the ultimate units in it.

DIAGRAM ILLUSTRATING HARRIS' METHOD

(2) p_1 C_{p1}	(2) p_2 C_{p1}	(4) p_3 C_{p2}	(6) p_4 C_{p2}
(3) p_5	(3) p_6	(6) p_7	(4) p_8
(3) p_9 C_{p3}	(3) p_{10} C_{p3}	(5) p_{11} C_{p4}	(5) p_{12} C_{p4}
(5) p_{13}	(5) p_{14}	(4) p_{15}	(4) p_{16}

$$\begin{aligned}
 p &= \text{Average yield of all ultimate units} = 4 \\
 n &= \text{Number of units in each group} = 4 \\
 m &= \text{Number of groups} = 4 \\
 S(p^2) &= \text{Sum of squares of the yields assigned} \\
 &\quad \text{for ultimate units} = 280 \\
 S(C_p^2) &= \text{Sum of squares of the group yields} = 1,080 \\
 \sigma_p &= \text{Standard deviation of assigned yield} \\
 &\quad \text{for the ultimate units} = \sqrt{1.5} = 1.2247
 \end{aligned}$$

$$\sigma_p^2 = (1.2247)^2 = 1.4999$$

The numbers enclosed in parentheses represent assumed values (bushels per acre). Now according to the formula

$$r_{p_1 p_2} = \frac{\{[S(C_p^2) - S(p^2)]/m[n(n-1)]\} - p^2}{\sigma_p^2}$$

Where $r_{p_1 p_2}$ is the constant sought, S is indicative of summation, C_p the calculated values for the groups, p_1, p_2 , etc. the assigned values for the ultimate units, m the number of groups, n the number of units in each group, p the average value of all the ultimate units and σ_p their standard deviation; by substituting the given values, the coefficient of correlation may be derived.

$$r_{p1p2} = \frac{\{[1,080 - 280] \div 4[4(4 - 1)]\} - 4^2}{1 \ 2247^2}$$

$$r_{p1p2} = \frac{16 \ 6667 - 16}{1 \ 4999} = \frac{0 \ 6667}{1 \ 4999} = 0.444 \pm 0 \ 135^1$$

The magnitude of the coefficient obtained may be influenced by the size of the ultimate and group units, the nature of the character measured, and the variety or strain grown.

In the illustrative diagram the plots are arranged in fours in what Harris refers to as a 2-by-2 fold manner. In making a computation of this nature, the data are arranged first in a table consisting of horizontal and vertical rows. The horizontal rows are referred to first. A grouping, therefore, of two horizontal and one vertical row would be a 2-by-1 fold.

In a study conducted in West Virginia, yields of oat hay and of wheat grain obtained from 270 plots were used. The area of each plot was 68 by 21 feet and in the case of wheat the plot yields were based upon five rod-row samples. Several methods of computation were used. In addition to the method outlined by Harris, in which computations were based upon a 2-by-2 fold and a 2-by-3 fold grouping, correlations were determined for adjacent plots in the ordinary manner. In one case the yields of plot 1 were correlated with 2, 2 with 3, 3 with 4, etc., where the pairs were adjacent. In the second method each plot was used only once as 1 with 2, 3 with 4, etc. The results were presented as "all contiguous plots" and "paired contiguous plots," respectively. The correlations for oat hay and for wheat grain are given in the following tables:

TABLE X.—CORRELATIONS FOR SOIL HETEROGENEITY BASED UPON THE YIELDS OF OAT HAY

Method of calculation	<i>n</i>	<i>r</i>
Harris, 2-by-2 fold	260	+0.631 ± 0.025
Harris, 2-by-3 fold	258	0.542 ± 0.030
Ordinary "all contiguous plots"	250	0.668 ± 0.024
Ordinary "all paired plots"	130	0.694 ± 0.031

TABLE XI.—CORRELATIONS FOR SOIL HETEROGENEITY BASED UPON THE YIELDS OF WHEAT GRAIN

Method of calculation	<i>n</i>	<i>r</i>
Harris, 2-by-2 fold	260	0.565 ± 0.028
Harris, 2-by-3 fold	258	0.516 ± 0.031
Ordinary "all contiguous plots"	250	0.553 ± 0.030
Ordinary "all paired plots"	130	0.617 ± 0.037

$$^1 \text{ P. E. coefficient of correlation} = \frac{\pm 0.6745(1 - r^2)}{\sqrt{n}} =$$

$$\frac{\pm 0.6745(1 - 0.444^2)}{\sqrt{16}} = \pm 0.135.$$

It is apparent that in these cases there is little difference in the size of the correlation coefficients whether Harris' method or either of the others are used.

The methods outlined are useful where it is desirable to determine the relative heterogeneity of several fields. In applying the tests as outlined, it is necessary to crop the field to a single variety. -

Estimating Soil Heterogeneity while Conducting Strain Trials.—

In case it is desired to compare the heterogeneity of two or more fields and, at the same time, conduct strain yield trials, it is necessary to sow the fields to be compared with the same sort of crop. For example, if a comparison of oat yields is to be made, it is desirable to include check plots of the same standard sort in both fields at the same distances apart and at regular intervals. The relative heterogeneity of the two fields may be determined by the use of yields obtained from the check plots and by computations of the coefficients of variability. The field in which the coefficient of variability proves to be the largest is considered the least desirable.

By a slight modification of the plan it is possible to compare the heterogeneity of two fields by means of correlation coefficients providing each field is planted in the same order and to the same strains. Four systematically distributed plots are used, as a rule, in the rod-row trials conducted at University Farm. The strains are repeated in the same order in each replication. To obtain the heterogeneity coefficient the average yield of each strain in the trial was considered as 100. The yielding ability of each plot was obtained by dividing its actual yield by the average yield of all four replicates and expressing the result in percentage. By the ordinary method, the correlations in yielding ability of adjacent plots or of plots at any distance apart were determined. Harris' method could likewise have been used.

The order of planting, the original yields and the calculated percentage yields of spring wheat for rod-row trials conducted at University Farm in 1925 are presented in the following table:

TABLE XII.—YIELDS OF ROW-TRIALS OF SPRING WHEAT IN 1925 AND PERCENTAGE YIELDS ON THE BASIS OF 100 PER CENT AS THE AVERAGE YIELD OF EACH VARIETY¹

Variety	N S N	Repetitions, yields in bushels					Repetitions, yields in percentage			
		First	Second	Third	Fourth	Average	First	Second	Third	Fourth
Marquis	Check	37 8	24 8	33 2	39 0	33 7	106	70	91	110
Marquis × Kanred	132-5	37 7	10 0	39 0	39 3	39 0	97	103	100	101
Marquis × Kanred	138-11	12 0	33 3	34 5	30 8	35 2	119	95	98	88
Marquis × Kanred	139-11	39 3	47 0	37 6	38 4	10 6	97	116	93	95
Marquis × Kanred	139-14	27 2	32 4	37 1	31 1	32 0	85	101	117	97
Marquis × Kanred	II-17-2	35 8	32 5	30 6	42 2	35 3	101	92	87	120
Marquis	Check	37 1	38 7	35 4	32 9	36 0	105	109	100	93
Marquis × Kanred	II-17-3	32 9	37 5	31 5	39 0	35 2	93	107	89	111
Marquis × Kanred	II-17-4	37 8	33 9	33 1	36 0	35 3	107	96	95	102
Marquis × Kanred	II-17-11	42 7	33 7	31 9	12 1	38 1	111	88	91	110
Marquis × Kanred	II-17-16	46 1	38 6	35 2	37 8	39 4	117	98	89	96
Marquis × Kanred	II-17-22	41 0	35 0	30 8	38 9	36 1	113	96	85	107
Marquis	Check	37 6	35 0	33 1	32 3	34 6	106	99	91	91
Marquis × Kanred	II-17-23	34 3	10 5	31 9	37 9	36 9	93	110	95	103
Marquis × Kanred	II-17-25	30 5	36 5	32 7	37 7	34 4	89	106	95	110
Marquis × Kanred	II-17-28	29 1	39 0	30 9	13 4	35 6	82	110	87	122
Marquis × Kanred	II-17-36	33 8	35 3	36 5	17 8	38 1	88	92	95	125
Marquis × Kanred	II-17-37	32 1	38 6	35 5	47 7	38 5	83	100	92	124
Marquis	Check	30 4	31 7	36 9	37 1	34 9	86	98	101	105
Marquis × Kanred	II-17-40	38 2	44 1	38 0	11 1	10 1	95	109	94	102
Marquis × Kanred	II-17-43	39 2	31 5	39 2	42 9	39 0	101	88	101	110
Marquis × Kanred	II-17-45	35 2	31 9	36 8	13 6	37 6	91	93	98	116
Marquis × Kanred	II-18-8	40 3	13 2	37 0	11 3	41 2	98	105	90	108
Marquis × Kanred	II-18-13	29 9	32 6	33 1	11 5	35 0	85	93	95	127
Marquis	Check	40 9	34 5	36 0	47 0	39 6	115	97	101	132
Marquis × Kanred	II-18-14	31 7	39 3	38 6	16 4	39 0	81	101	99	119
Marquis × Kanred	II-18-46	37 6	37 2	40 8	15 6	10 3	93	92	101	113
Marquis × Kanred	II-18-47	33 8	36 5	31 8	11 8	36 7	92	99	95	114
Marquis × Kanred	II-18-48	37 8	32 7	36 3	31 1	35 2	107	93	103	97
Marquis × Kanred	II-18-49	37 6	30 7	14 0	36 9	37 3	101	82	118	99
Marquis	Check	38 9	30 3	12 7	34 4	36 3	110	85	120	94
Marquis × Kanred	II-18-50	40 7	29 8	32 5	29 6	33 2	123	90	98	89
Marquis × Kanred	II-18-51	44 8	32 7	34 6	38 9	37 8	119	87	92	103
Kota Natural Cross	II-19-2	37 1	35 0	37 5	33 6	35 8	104	98	105	94
Kota Natural Cross	II-18-16	31 0	34 4	35 0	31 8	33 8	92	102	101	103
Kota Natural Cross	II-18-17	36 5	38 9	37 5	40 9	38 5	95	101	97	106
Marquis	Check	33 6	27 0	34 9	35 9	32 0	95	76	98	101
Kota Natural Cross	II-18-19	29 3	30 4	39 1	30 9	32 4	90	94	121	95
Kota Natural Cross	II-18-20	36 2	41 2	42 0	30 8	37 6	96	110	112	82
Kota Natural Cross	II-18-21	39 6	33 0	35 1	28 1	31 0	110	97	103	84
Kota Natural Cross	II-18-28	40 5	35 5	42 1	33 3	37 9	107	94	111	88
Kota Natural Cross	II-18-31	37 5	37 3	36 1	32 4	35 8	105	104	101	91
Marquis	Check	39 4	34 2	36 7	28 3	31 7	111	96	103	80
Kota Natural Cross	II-18-33	36 8	35 2	33 6	32 5	34 5	107	102	97	94
Kota Natural Cross	II-18-37	29 0	29 6	27 1	32 0	29 4	99	101	92	109
Kota Natural Cross	II-18-56	44 2	41 0	33 9	37 5	39 2	113	105	86	96
Kota × Ruby	II-19-23	25 8	33 7	32 5	33 3	31 3	82	108	104	106
Kota × Ruby	II-19-26	35 9	37 1	33 2	32 6	34 8	103	107	95	94
Marquis	Check	42 2	34 2	37 6	40 0	38 5	119	96	106	113
Kota × Ruby	II-19-42	35 6	29 7	36 2	36 0	34 4	103	86	105	105
Kota × Ruby	II-19-43	33 4	31 5	31 9	27 9	31 9	105	99	109	87
Kota × Ruby	II-19-44	36 1	33 2	29 1	32 8	32 8	110	101	89	100
Kota × Ruby	II-19-48	34 4	32 6	33 4	38 3	34 7	99	94	96	110
Kota × Ruby	II-19-49	36 5	34 4	33 2	38 0	35 5	103	97	94	107
Marquis	Check	29 9	33 5	32 1	33 5	32 3	81	94	90	94
Kota × Ruby	II-19-54	27 1	34 5	32 1	38 3	33 0	82	105	97	110
Kota × Ruby	II-19-55	27 8	32 5	31 4	44 5	34 1	82	95	92	130
Kota × Ruby	II-19-34	35 4	32 7	32 2	39 2	34 9	101	94	92	112
Kota × Ruby	II-19-39	30 8	34 9	33 2	42 5	35 4	87	99	94	120
Kota × Ruby	II-19-40	36 5	32 8	29 2	41 3	35 0	104	94	83	118

TABLE XII.—(Continued)

Variety	N. S. N.	Replications, yields in bushels					Replications, yields in percentage			
		First	Sec- ond	Third	Fourth	Average	First	Sec- ond	Third	Fourth
Marquis.....	Check	35.9	31.1	39.1	35.1	35.3	101	88	110	99
Marquis × Kota.....	II-19-9	41.1	35.0	33.4	37.7	36.8	112	95	91	102
Marquis × Kota.....	II-19-11	34.1	35.8	36.4	36.9	35.8	95	100	102	103
Marquis × Kota.....	II-19-45	25.3	27.7	40.9	32.7	31.7	80	87	129	103
Marquis × Kota.....	II-19-46	42.4	37.3	44.9	39.2	41.0	103	91	110	96
Marquis × Kota.....	II-19-47	36.2	32.3 ^m	37.0	38.4	36.0	101	90 ^m	103	107
Marquis.....	Check	32.7	33.0 ⁿ	43.6	36.8	36.5	92	93 ⁿ	123	104
Marquis × Kota.....	II-19-51	39.3	37.0	35.2	37.8	37.6	105	101	94	101
Marquis × Kota.....	II-19-53	37.7	36.1	32.5	39.4	36.4	104	99	89	108
Marquis × Kota.....	II-19-57	37.0	39.3	44.8 ⁿ	36.9	39.5	94	99	113 ⁿ	93
Marquis × Tumillo.....	II-15-43	29.9	27.1	44.9 ⁿ	34.1	34.0	88	80	132 ⁿ	100
Marquis × Tumillo.....	II-15-44	37.1 ^r	27.7	42.0	35.6	35.6	104 ^r	78	118	100
Marquis.....	Check	46.8 ^r	32.1	41.1	37.2	39.3	132 ^r	90	116	105
Marquis × Tumillo.....	II-15-51	35.9	31.7	32.9	27.9	32.1	112	99	102	87
Marquis × Preston.....	II-15-8	38.5	36.8	45.4	38.9	39.9	96	92	114	97
Marquis × Preston.....	II-15-13	36.1	34.7	40.1	37.2 ^{ab}	37.0	98	94	108	101 ^{ab}
Marquis × Preston.....	II-15-16	37.6	31.0	35.3	45.2 ^c	37.3	101	83	95	121 ^c
Marquis × Preston.....	II-15-24	41.1	40.4	43.1	34.4	39.8	103	102	108	86
Marquis.....	Check	34.3	38.2	43.7	33.4	37.4	97	108	123	94
Marquis × Bluestem.....	II-15-39	38.9	39.1	38.7	28.0	36.2	107	108	107	77
Marquis × Bluestem.....	II-15-41	40.9	36.0	41.4	31.6	37.5	109	96	110	84
Marquis × Kota.....	N.D. 1656	39.9	40.2	41.2	36.5	39.5	101	102	104	92
Ceres.....	N.D. 1658	39.8	41.9	38.5	30.7	37.7	106	111	102	81
Kota (Army's).....	Bulk	39.0	37.4	40.3	28.5	36.3	107	103	111	79
Marquis.....	Check	34.6	30.1	28.5	32.4	31.4	97	85	80	91
Mindum.....	I-00-52	39.7	43.2 ^d	39.7	32.3	38.7	103	112 ^d	103	83
Pentad.....	III-17	28.2	40.7 ^e	31.1	30.2	32.6	87	125 ^e	95	93
Parker's Marquis.....	III-25	27.8	35.6	35.6	30.3	32.3	86	110	110	94
Dicklow × Sevier.....	G. 40	25.2	20.3	22.1 ^f	20.0	21.9	115	93	101 ^f	91
Dicklow × Sevier.....	G. 149	29.0	19.8	30.7 ^g	24.6	26.0	112	76	118 ^g	95
Marquis.....	Check	36.3	35.1	33.5	32.7	34.4	102	99	94	92

¹ In computing the percentage yields of the check plots, the average yield of all checks which was 35.5 bushels was used.

^a End of series 1.

^b Beginning of series 2.

^c Center of series 2.

^d End of series 2.

^e Beginning of series 3.

^f Center of series 3.

^g Center of series 4.

^h End of series 4.

^k Beginning of series 5.

^l Center of series 5.

^m End of series 5.

ⁿ Beginning of series 6.

^o Center of series 6.

^p End of series 6.

^q Beginning of series 7.

^r Center of series 7.

^s End of series 7.

^t Beginning of series 8.

^u Center of series 8.

^v End of series 8.

^w Beginning of series 9.

^x Center of series 9.

^y End of series 9.

^z Beginning of series 10.

^{aa} Center of series 10.

^{bb} End of series 10.

^{cc} Beginning of series 11.

A dead furrow marked the center of each series.

In this problem certain plots which were near the ends or centers were not used in the correlation. While the location of plots in each series was known approximately, the number of strains in each series deviated slightly, so that, for example, it is possible that check plot designated by *b* may have been in series 1 instead of at the beginning of series 2. The plots, therefore, at the left and right of the plots designated as the end, center, and beginning of each series were not used in the correlations. There were a few intervening rows between the end of the first series and the beginning of the second, therefore, in this study it was impossible to correlate varieties of the first series with those of the second.

The data arranged in the form of a correlation surface and the correlation coefficient for plots separated by four intervening plots are presented in Table XIII. The method of entering results in the correlation table for plots separated by four intervening plots may be illustrated by starting at the beginning of the first series of the first replications, and by using percentage yields. The following pairs were correlated—106 with 101, 97 with 105, 119 with 93, 97 with 107, 85 with 111, 89 with 95, etc. The calculated coefficient was $r = +0.096 \pm 0.049$, which shows little or no soil heterogeneity for plots separated by four intervening plots.

The correlations obtained in a similar manner for adjacent plots and for plots located at less than four plots from each other were between 0.3 and 0.2, respectively, which indicated a low degree of soil hetero-

TABLE XIII—CORRELATION IN YIELDING ABILITY OF PLOTS SEPARATED BY FOUR INTERVENING PLOTS IN SPRING WHEAT ROW-ROW TRIALS UNIVERSITY FARM, 1925

Percentage classes for yielding ability

	75	78	81	84	87	90	93	96	99	102	105	108	111	114	117	120	123	126	129	132	
75											1										1
78			1		2																3
81						4				3	1		1								9
84			1			1	1	1		2	1	2	2								11
87			1	1			3	1		1	1	1	1								9
90	1			1			1	2		1	1		1				1				9
93		1			1	2	7	2	2	2		2	1		1	1	1			1	24
96			1		1		4	2	2	1	5	5	4		1						26
99					1		3		4	3	2	3	2								18
102			1		1		5	3	1	4	3	1	1				1			1	22
105			1		2		2	2	3		1	1							1		13
108			1		1		2	1	3	1			1	3			1				14
111					2	1	1	1	1	5						2					13
114						1				2		1									4
117							1	1				1		1							1
120							2	1		2											5
123												1	1								2
126								1													1
129																					0
132										1											1
																					189

$r = 0.090 \pm 0.049$

geneity. In 1924, however, the extent of heterogeneity was much greater for the spring-wheat and oats plots than in 1925, the studies being conducted in near-by fields for 1924 and 1925. The fields are set aside for nursery trials and are under a systematic rotation. The winter-wheat trials are conducted in a different field. Correlation coefficients, which express the extent of heterogeneity for 1924, are given in the following table:

TABLE XIV.—CORRELATION OF PERCENTAGE YIELDING ABILITY IN NEAR-BY PLOTS OF OATS, WINTER WHEAT, AND SPRING WHEAT, 1924

Crop	Correlation of	Correlation coefficient
Oat rod rows.....	Adjacent plots	0.572 ± 0.025
	Separated by one	0.490 ± 0.029
	Separated by two	0.407 ± 0.034
	Separated by three	0.412 ± 0.035
	Separated by four	0.264 ± 0.041
	Separated by ten	0.275 ± 0.057
Spring-wheat rod rows.....	Adjacent plots	0.618 ± 0.023
	Separated by one	0.518 ± 0.028
	Separated by two	0.454 ± 0.030
	Separated by three	0.383 ± 0.034
	Separated by four	0.449 ± 0.034
Winter-wheat rod rows.....	Separated by ten	0.429 ± 0.060
	Adjacent rows	0.552 ± 0.068
	Separated by one	0.293 ± 0.028
	Separated by four	-0.114 ± 0.118

The tests with spring and winter wheat and oats were conducted on different fields, as has been mentioned. With winter wheat the soil heterogeneity appeared to be expressed only in near-by plots. With spring wheat and oats considerable heterogeneity was present in plots which were at some distance from each other. In other words there was considerable systematic variation across the field. By placing the same strain tests on separate fields and by the method outlined the relative heterogeneity of the two areas could be determined and at the same time yield trials could be conducted.

Use of Check Plots in Correcting Yields.—Aside from their use to indicate soil variation, check plots have often been used to make direct corrections for yield. Table XV, taken from Wood and Stratton (1910), illustrates a simple use of checks for the purpose of correcting yields where there is a tendency to vary in one direction across a field.

In the second column of Table XV the actual yields are given of 25 contiguous $\frac{1}{2}$ -acre plots across a field. The figures show a more or less gradual decrease, reading from top to bottom.

There is a difference of 500 pounds between the average yield of the first five plots and the average yield of the last five plots, or an average difference from plot to plot of 25 pounds. This correction is applied by adding to those on one side and subtracting from those on the other side of the centrally located plot. The amount added or subtracted depends on the distance from the center, *i.e.*, a progressive difference of 25 pounds for each plot in either direction from the central one. The corrected yields are found in the last column of the table. Note that the probable error is 3 per cent less in the corrected than in the uncorrected yields.

TABLE XV.—DIRECT CORRECTION FOR YIELD WHERE VARIATION IS IN ONE DIRECTION ACROSS A FIELD

	Yield of $\frac{1}{2}$ acre plots, pounds	Correction, pounds	Corrected yields, pounds
Mean 2,640	$\left\{ \begin{array}{l} 2,537 \\ 2,515 \\ 2,866 \\ 2,648 \\ 2,636 \\ 2,581 \\ 2,814 \\ 2,944 \end{array} \right.$	$\left\{ \begin{array}{l} -12 \times 25 \\ -11 \times 25 \\ -10 \times 25 \\ -9 \times 25 \\ -8 \times 25 \\ -7 \times 25 \\ -6 \times 25 \\ -5 \times 25 \end{array} \right.$	$\left\{ \begin{array}{l} 2,237 \\ 2,240 \\ 2,616 \\ 2,423 \\ 2,436 \\ 2,406 \\ 2,664 \\ 2,819 \end{array} \right.$
Difference between means 500 pounds	$\left\{ \begin{array}{l} 2,748 \\ 2,593 \\ 2,567 \\ 2,357 \\ 2,415 \end{array} \right.$	$\left\{ \begin{array}{l} -4 \times 25 \\ -3 \times 25 \\ -2 \times 25 \\ -1 \times 25 \\ 0 \times 25 \end{array} \right.$	$\left\{ \begin{array}{l} 2,648 \\ 2,518 \\ 2,517 \\ 2,332 \\ 2,415 \end{array} \right.$
Correction from plot to plot $\frac{500}{20} = 25$ pounds	$\left\{ \begin{array}{l} 2,424 \\ 2,423 \\ 2,399 \\ 2,272 \\ 2,374 \\ 2,123 \\ 2,273 \end{array} \right.$	$\left\{ \begin{array}{l} +1 \times 25 \\ +2 \times 25 \\ +3 \times 25 \\ +4 \times 25 \\ +5 \times 25 \\ +6 \times 25 \\ +7 \times 25 \end{array} \right.$	$\left\{ \begin{array}{l} 2,449 \\ 2,473 \\ 2,474 \\ 2,372 \\ 2,499 \\ 2,273 \\ 2,448 \end{array} \right.$
Mean 2,140	$\left\{ \begin{array}{l} 2,117 \\ 2,001 \\ 2,115 \\ 2,246 \\ 2,222 \end{array} \right.$	$\left\{ \begin{array}{l} +8 \times 25 \\ +9 \times 25 \\ +10 \times 25 \\ +11 \times 25 \\ +12 \times 25 \end{array} \right.$	$\left\{ \begin{array}{l} 2,317 \\ 2,226 \\ 2,365 \\ 2,521 \\ 2,522 \end{array} \right.$
	P. E. ± 7 per cent	.	P. E. ± 4 per cent

The method outlined above may be used only where there is a comparatively large number of similarly treated plots and where the increase or decrease in yield across a field is fairly consistent. If check plots are grown every third to fifth plot as they frequently are, a direct correction for yield is sometimes made as follows:

DIAGRAM ILLUSTRATING DISTRIBUTION OF CHECKS

C_1	1	2	3	C_2	4	5	6	C_3
-------	---	---	---	-------	---	---	---	-------

Suppose every fourth plot is a check. The productivity of each intervening plot is estimated on the basis of the yields of the two nearest checks. For instance, the true productivity of plot one is assumed to equal $\frac{3}{4}C_1 + \frac{1}{4}C_2$; for plot two equals $\frac{1}{2}C_1 + \frac{1}{2}C_2$; and for plot three equals $\frac{1}{4}C_1 + \frac{3}{4}C_2$; etc. The yielding value of plot six in

terms of the yield of check plots could be calculated by dividing the sum of one-fourth the yield of C_2 and three-fourths the yield of C_3 by the average yield of all checks and expressing the relationship in percentage. The corrected yield of plot six would be obtained by dividing the actual yield by the computed percentage yield. This method assumes perfect correlation between the yielding value of near-by plots which probably very seldom is obtained in actual practice. This method and any other methods as yet devised for correcting yields assumes that all varieties respond in the same relative manner to various environmental influences which, in some cases, is not a sound conclusion from a biological standpoint.

Several other formulae have been used to calculate the normal yields or (N) of plots adjacent to a particular check. In these formulae, C = average yield of all checks, C_1 , C_2 , etc. equal the yield of particular check plots. In formulae (1) and (3), as given, the check plots were arranged every third plot. The formulae may be modified in relation to the distance between the check plots.

Some of the formulae tried are:

$$\begin{aligned}\frac{1}{2}(C + 2\frac{2}{3}C_1 + \frac{1}{3}C_2) &= N & (1) \\ \frac{1}{2}(C + C_1) \text{ or } \frac{1}{2}(C + C_2) &= N & (2) \\ \frac{1}{4}[p_1C + p_2(2\frac{2}{3}C_1 + \frac{1}{3}C_2)] &= N & (3)\end{aligned}$$

where p_1 and p_2 are equal to 1 the numerical values and 3, respectively.

Each of the above formulae corrects on the basis of partial relationship or partial correlation between near-by plots. This is evident as in each case the average yield of all checks is used together with the yield of near-by checks to obtain an idea of normal yielding ability of the plot in question. The use of the above formulae as the means of adjusting yields were compared by Stockberger (1916) for yield of hops and by Batchelor and Reed (1918) for yields of 10-tree navel orange plots with the method of direct correction based upon the yields of near-by checks. Each of the three methods of correction gave lower average deviation values than the direct method of correction based upon near-by checks.

Richey (1924) devised a method of planting by which each of ten strains in the comparison was used as a check in some one of the ten replications. The heterogeneity coefficient was computed and adjustment of the yields of near-by plots made upon the basis of a moving average and the regression equation. A somewhat similar method has been tried in rod-row trials. This method can be illustrated by the studies of heterogeneity reported in Table XIV. After computing the correlation coefficients which express the degree of heterogeneity, the regression equations were calculated by means of which any particular value of Y can be computed for any value of X . The means, standard deviations,

and regression equations for plots located adjacent to each other and separated by one to four intervening plots are given in the following table:

TABLE XVI.—MEANS, STANDARD DEVIATIONS, AND REGRESSION EQUATIONS
OBTAINED FROM THE CORRELATION STUDIES OF THE YIELDING
ABILITY OF SPRING WHEAT ROW ROWS
University Farm, 1924

Based on correlation of	Means		Standard deviations		Regression equations
	X	Y	X	Y	
Adjacent plots . . .	99 74	99 74	13 90	13 95	$Y = 37.85 + 0.6205X$
Separated by one . . .	99 76	99 77	14 02	14 05	$Y = 47.99 + 0.5191X$
Separated by two . . .	99 74	99 90	14 16	14 18	$Y = 54.56 + 0.4546X$
Separated by three . . .	99 75	99 93	14 32	14 48	$Y = 61.30 + 0.3873X$
Separated by four . . .	99 84	100 00	14 40	13 95	$Y = 56.72 + 0.4350X$

In the spring-wheat and oats studies, check plots of standard varieties were distributed through the test such that every sixth plot was a check. The yields of each plot of near-by varieties were adjusted by means of the regression values. The method used is illustrated for several plots in the wheat series.

Plot No.	Actual yield	Percentage yield
Check <i>a</i>	25 1	93
8	27 5	
9	20.3	
10	28 3	
11	24 2	
12	25 7	
Check <i>b</i>	32 2	120

The yielding ability of each check plot was expressed in percentage by dividing its actual yield by the average of all check plots. By this method the yielding ability of Check *a* was 93 and of *b* 120.

If y equals percentage yield of near-by plot and x equals percentage yield of the check, then the corrected percentage yielding values for plot 8 would be

$$1. Y = 37.85 + 0.6205 X = 95.56$$

$$2. Y = 56.72 + 0.4350 X = 108.92$$

A value of 102 was obtained by adding 1 and 2 and averaging. The corrected yield for plot 8 in bushels would then be obtained by dividing the actual yield, 27.5 bushels, by 102. In this way the yield of each plot

of each variety was adjusted by the yield of the two nearest check plots on the basis of the average relationship as expressed by the calculated regression equations.

After obtaining a corrected yield for each plot of all varieties, except the check plots, a probable error in percentage was calculated by the deviation from the mean method. These probable errors were then compared with probable errors obtained before adjustment. The results are presented in the following table.

TABLE XVII.—PROBABLE ERROR FOR A SINGLE PLOT TEST BEFORE ADJUSTMENT OF YIELDS AND AFTER CORRECTING YIELDS ON THE BASIS OF THE REGRESSION VALUES AND IN RELATION TO THE TWO NEAREST CHECK PLOTS

Crop	Probable error in percentage	
	Actual yield	After correction
Spring wheat.....	9.9	8.0
Oats.....	6.7	5.8

The actual percentage probable errors are reduced by adjustment to a moving average by approximately 19 and 13 per cent, respectively, which is slightly more than expected on the basis of the standard errors of estimate for the correlation coefficients obtained. It seems very doubtful whether the reduction in probable error is worth the trouble of making the calculations.

Some Difficulties of Field Trials.—From the previous discussion, it is apparent that there are many difficulties in making accurate field trials. There are numerous reasons for this. When large numbers of strains must be compared, each strain must be grown in small plots. The difficulties of planting, harvesting, and threshing the crops on small plots and of obtaining yields indicative of the probable yielding ability, when planted under farm conditions, are rather great. The rod-row method for small grains, which will be presented in some detail later, appears fairly satisfactory for these crops. Even here there is not complete uniformity of opinion as to rate and methods of planting and other details of handling. It is probable that, under different environmental conditions, it will be found necessary to modify the general methods used. The better methods of work must be learned, therefore, for each separate locality. General principles can be laid down, however, for such important questions as shape and size of plot and the number of replications to be used, and, likewise, for competition between near-by varieties.

Replication and Its Value.—It has been found that systematic repetition of the plots reduces the probable error and, hence, increases the

significance of the results. The number of replications necessary in order to make reliable comparisons is somewhat dependent on the kind of crop but to a greater extent on soil heterogeneity. If it were desired to establish a significant difference of as little as 2 bushels between varieties, more replications would be needed than if a significant difference of 4 bushels was accepted as satisfactory. Several investigations have been reported which for the particular condition of the experiment show the number of replications desirable.

Mercer and Hall (1911), of England recommend the use of five systematically distributed plots of $\frac{1}{40}$ acre each. Montgomery (1913), in his work at Nebraska, found that 16-foot rows gave best results when repeated from 10 to 20 times. At the Cornell Experiment Station, when a careful yield test is desired, each strain is grown in 10 distributed rod rows.

In the plant-breeding nurseries of the Minnesota and West Virginia Experiment Stations, the practice is followed of growing each strain in a plot consisting of three rod rows. The plots are replicated three times, making four plots in all. The central rows only are harvested. Table XVIII, taken from Hayes and Army (1917), shows the effect of replication based on the yield of the central rows of the wheat checks grown in 1916.

TABLE XVIII.—VALUE OF REPLICATION BASED ON 72 CENTRAL ROWS OF 3-ROW PLOTS OF TURKEY WINTER WHEAT (MINN. 529) GROWN IN THE PLANT-BREEDING NURSERY

Number of replications	Number of variables	Mean yield per acre	Standard deviation
None	72	27.5 ± 0.4	4.65 ± 0.26
One (average of two plots)	36	27.6 ± 0.3	2.98 ± 0.24
Two (average of three plots)	24	27.4 ± 0.3	2.51 ± 0.24
Three (average of four plots)	18	27.6 ± 0.2	1.49 ± 0.17
Five (average of six plots)	12	27.3 ± 0.4	2.01 ± 0.28
Eleven (average of twelve plots)	6	27.3 ± 0.3	1.21 ± 0.24

While the standard deviations do not decrease according to theoretical expectation, they do show a marked decrease up to and including three replications. In general, beyond this point it is questionable whether the relatively small gain in accuracy warrants the additional work. Other results obtained at the Minnesota Station indicate that plots of three rod rows each or $\frac{1}{40}$ -acre plots sown with the ordinary grain drill, give about as accurate a comparison for yield when replicated three times as when replicated eight times.

The illustration of the value of replications in which yields of check plots and the same amount of land used for the study of the value of a single-plot test as for several replications, introduces an error which is not warranted. It is a matter of common experience that small areas of land are more uniform as a rule than larger areas. The larger the number of replications, however, the greater the area of land which must be available and, consequently, the greater the deviations in productivity.

Professor A. C. Arny has conducted several studies of field-plot technic and kindly furnished yield data for 120 rod rows of Haynes Bluestem wheat. The following computations illustrate the value of replication. The data on yield, for row 1 to row 120, respectively, are given on the basis of bushels per acre and are as follows:

Yields obtained in rod rows:

25.0, 22.0, 21.7, 22.0, 18.6, 23.5, 20.3, 19.9, 24.9, 22.9, 22.9, 25.0,
24.9, 25.0, 20.7, 24.5, 26.3, 25.2, 25.6, 23.1, 28.5, 27.0, 26.6, 25.9,
29.4, 24.4, 23.1, 30.7, 25.7, 21.9, 23.2, 23.2, 21.5, 25.6, 24.4, 28.2,
28.7, 26.8, 25.2, 29.6, 25.4, 26.5, 24.4, 24.1, 29.2, 24.3, 28.9, 25.5,
28.0, 23.7, 26.4, 27.8, 23.8, 23.7, 28.3, 28.8, 21.0, 23.8, 24.8, 22.8,
27.0, 23.8, 24.6, 31.7, 28.0, 28.1, 24.5, 26.7, 31.6, 23.7, 25.0, 33.0,
28.9, 27.5, 25.2, 27.9, 28.2, 25.4, 25.8, 28.1, 32.0, 29.6, 28.3, 33.7,
30.9, 27.2, 26.0, 30.0, 22.7, 21.6, 19.3, 24.0, 28.8, 25.2, 26.0, 27.6,
25.3, 27.4, 25.2, 21.6, 28.3, 25.1, 21.6, 24.6, 25.9, 24.8, 26.9, 25.9,
24.1, 25.8, 22.1, 26.9, 27.6, 27.6, 27.3, 30.2, 22.4, 23.7, 23.1, 26.5.

For the purpose of studying the value of replication the variability of yields was computed separately on the basis of 20 determinations and for one, two, four, and six systematically distributed plots.

The coefficients of variability are compared in the following table with the mathematical expectation:

TABLE XIX.—THE VALUE OF REPLICATION IN ROD-ROW TRIALS AS A MEANS OF REDUCING THE DEGREE OF VARIABILITY

Number of determinations	Number of systematically distributed plots	C. V.	Mathematical expectation
20	1	9.05	9.05
20	2	6.54	$9.05/\sqrt{2} = 6.42$
20	4	5.61	4.53
20	6	4.44	3.69

The calculated coefficient of variability decreases in size as a result of replication, although slightly less rapidly than would be indicated by mathematical expectation. This is, perhaps, because a greater area of land must be used for several replications than can be used for single-

plot trials, which on the average brings in soils of greater difference in productivity than found in smaller areas.

An illustration of the value of replication with strawberries has been furnished by A. N. Wilcox. In this study $\frac{1}{3}$ 20-acre plots were used and the computations were based on 20 determinations, the original yields of fruit being obtained from 80 single-row plots. As there were four separate computations for the use of single plots, a diagram of the field is included.

DIAGRAM OF PLOTS OF A STRAWBERRY FIELD

1	41
2	12
etc.	etc.
(a)	(c)
21	61
22	62
etc.	etc.
(b)	(d)

The coefficients of variability are presented in the following table:

TABLE XX.—THE VALUE OF REPLICATION IN STRAWBERRIES (After A. N. Wilcox)

Area of field	Number of determinations	Number of systematically distributed plots	C. V.	Average C. V. of group	Mathematical expectation
a	20	1	16.93 \pm 1.86	19.6	19.6
b	20	1	24.33 \pm 2.75		
c	20	1	14.77 \pm 1.60		
d	20	1	22.23 \pm 2.49		
a and b	20	2	11.97 \pm 1.29	14.6	13.9
c and d	20	2	17.25 \pm 1.90		
a, b, c, and d	20	4	10.92 \pm 1.18	10.9	9.2

Replication was found in this case to be a promising means of controlling soil heterogeneity. It does not always control heterogeneity for the area of land upon which some of the replications are carried may be very different from the remainder of the field and the larger the area the more difficult it is to obtain similar growth conditions. By carrying check plots at frequent intervals and by studying the two varieties on the basis of the probable error of the differences (essentially the same thing as using the correlation coefficient in the correct formula for probable error of a difference) when similar plots are paired, it is possible to control

soil heterogeneity by replication and practically to reduce the error of the test to a point, limited only by expense and available land.

The manner of making replications is another factor to be considered. If the experimental plots are all planted in a single series, then replication becomes a matter of systematic repetition, as is shown by the following diagram in which each different letter represents a distinct strain:

A METHOD OF REPLICATION

A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H
---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

As a rule the experimental plots cannot all be placed in the same series. It is often necessary to make alterations from a mere systematic repetition in order to secure a representative distribution of the strains. The two following diagrams illustrate a correct and an incorrect manner of replication:

CORRECT MANNER OF REPLICATION

A	J	G	D
B	K	H	E
C	L	I	F
D	A	J	G
E	B	K	H
F	C	L	I
G	D	A	J
H	E	B	K
I	F	C	L
J	G	D	A
K	H	E	B
L	I	F	C

INCORRECT MANNER OF REPLICATION

A	A	A	A
B	B	B	B
C	C	C	C
D	D	D	D
E	E	E	E
F	F	F	F
G	G	G	G
H	H	H	H
I	I	I	I
J	J	J	J
K	K	K	K
L	L	L	L

Size of Plot.—The number of replications required to secure a given degree of accuracy is somewhat dependent on the area of the plot. Mercer and Hall (1911) found that variability is diminished with increased size of plot up to $\frac{1}{40}$ acre. Plots of larger area do not show the same relative reduction in variability. Figure 14 represents graphically their results with wheat.

Montgomery (1913) also finds that increased size of plot, up to a certain limit, rapidly decreases variability. In plant-breeding work, where very numerous strains are compared, the size of plot is necessarily limited by available space and sometimes by amount of seed. Some form of row planting is usually followed. These rows are planted, cultivated, and harvested by hand and frequently show nearly as low probable errors as those obtained from $\frac{1}{40}$ -acre field plots.

In one such study conducted by Prof. A. C. Arny with Haynes, Blue-stem wheat the probable error for rod-row trials was 11.30 per cent while that for $\frac{1}{40}$ -acre plots was 8.91 per cent

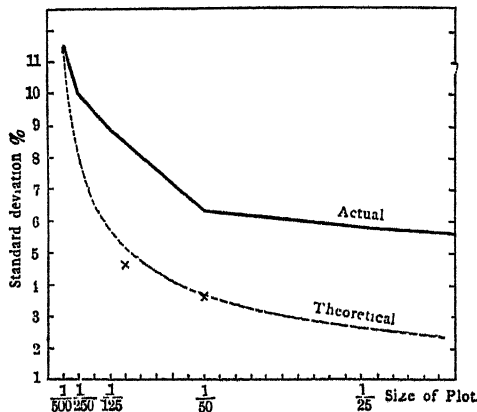


FIG. 14.—Actual and theoretical reduction in standard deviation due to increase in size of plot

Studies in rod-row trials indicate that size of plot is less important than replication as a means of controlling variability. The tests reported in the following table represent a 2-year average for studies of single- and two-row plots:

TABLE XXI.—COEFFICIENTS OF VARIABILITY FOR A COMPARISON OF THE VARIABILITY IN YIELDS OF SINGLE- AND OF TWO-ROW ROWS
University Farm

Variety	Num- ber of plots	Coefficient of variability	
		Single row	Two central rows
Manchuria, No. 105	36 5	15.89 ± 0.94	16.00 ± 0.93
Ligowa, No. 281	42.5	14.75 ± 0.74	12.84 ± 0.65
Haynes, No. 169	35 5	19.24 ± 0.94	15.27 ± 0.76

These studies were obtained from check plots of barley, oats, and wheat, respectively, which were spaced every fifth or sixth plot in the

experiment. They represent central rows, as border rows were included for each plot.

Similar results were obtained by Stadler 1921 in the following table:

TABLE XXII.—COEFFICIENTS OF VARIABILITY OF ONE- AND THREE-ROW PLOTS

Check plots of	Number of plots	Coefficient of variability	
		One central row	Three interior rows
Barley.....	21	24.80	22.18
Oats.....	20	24.80	22.59
Wheat.....	80	27.68	25.11

In a study of plot size with potatoes, conducted by Krantz (1922) at Minnesota, a comparison of relative variability for rows of lengths from one to six rods was made. As in most experiments, the entire area was used which makes the comparison somewhat more favorable for large plots than would be obtained in actual practice. It was concluded that a row three rods long was more desirable than a single-rod row and was about as valuable as a six-rod row. A study of plot size with potatoes has also been made at the West Virginia Station (Westover, 1924). In this experiment there were available 220 single-row plots 150 feet long. Each plot was sampled by taking the yield of various row lengths in multiples of 10 feet. The sharp reduction in the probable error occurred between row lengths of 10 and 40 feet. Beyond 60 feet the probable error was reduced very little. In a somewhat similar study, Batchelor and Reed concluded that an eight-tree plot for orchard crops was more desirable than one of smaller size.

It may be impossible to decide what size of plot is most advantageous without conducting the study under various experimental conditions and for special crops. In comparisons of F_1 crosses between relatively pure lines in corn, all plants of each F_1 cross consist approximately of the same genotype. It seems reasonable to conclude that in such comparisons smaller plots may prove as reliable as much larger ones where, in addition to soil variability, it is necessary to have sufficient plants in each plot in order to obtain a random genetic sample of the variety.

Shape of Plot and Border Effect.—Plants growing along the side or end of a plot are often more thrifty and vigorous than those growing in the interior. When plots consist of single rows, the plants at the extremities near the alleys or pathways appear superior to those growing farther in.

Mercer and Hall (1911) divided a field planted to a single variety into plots of equal area but different in shape (approximately, 20 by 12 and 50 by 5 yards) and, therefore, without border effect. No significant

difference in comparative variability was found between the two shapes. Barber (1914) found that where cultivated pathways surrounded plots, the plants along the margins were more productive than those within the plot.

Table XXIII presents data collected by Army and Hayes (1918) from plots seeded with a grain drill, in rows 6 inches apart. Eighteen-inch alleys separated the plots, and there was a roadway along each end. In length the plots were trimmed to 132 feet. They were 17 drill rows in breadth, each 6 inches apart. Each of the two outside border rows was harvested separately and the yield compared with the yields obtained from the central rows. The plants on each end of the plots to a depth of at least 1 foot were cut and discarded.

TABLE XXIII—COMPARISON OF AVERAGE YIELD OF OATS, WHEAT, AND BARLEY HARVESTED FROM BORDER ROWS AND CENTRAL ROWS

Plots 132 by 8.5 feet

Source	Oats		Wheat		Barley	
	Number of plots	Yield per acre, bushels	Number of plots	Yield per acre, bushels	Number of plots	Yield per acre, bushels
Outside border rows.	14	132 0	20	55 0	16	97 7
Inside border rows. . .	44	88 0	20	41 0	16	64.5
Central 13 rows. . .	44	71 4	20	27 5	16	42 9

It is clear that border effect may profoundly influence yield. Long, narrow plots have a larger proportion of their area in border than those which more nearly approach a square. This would seem to indicate that square plots should be given preference over oblong ones unless the borders are discarded. As a matter of fact, most workers use long, narrow plots because of the greater ease with which they may be seeded and harvested with machinery. Border effect may be entirely removed by discarding the borders and ends of the plot.

The removal of borders appears desirable when the fact is considered that different strains and varieties may react unequally to borders or ends. Evidence has been accumulated which shows that some strains utilize the border to a greater degree than others. Obviously, those strains which gain least from the alley space will not be given a fair trial unless border rows are discarded from all the plots in the experiment. Conversely, those which have the greater ability to use the border may be given a higher rating than they deserve unless the borders are removed.

It would seem from the evidence presented that it is highly desirable to discard ends and borders to a depth of at least 1 foot in the case of

rectangular plots and 1 foot at each end in the case of rod rows growing side by side.

At the West Virginia Station¹ the soybean varieties are grown in four-row plots and replicated three or more times. The rows are 18 feet long and 30 inches apart. After discarding the end plants one of the inner rows is harvested for seed and the other inner row is harvested for forage. A study has been made of the influence of height and yield of the adjacent rows on the yields of the border rows. No appreciable effect of competition was found.

Competition as a Factor in Plot Variability.—Competition between near-by strains, particularly under certain experimental conditions, may seriously influence results. A tall variety may hamper a short one, or a vigorous grower may inhibit one that grows more slowly. The existence of competition between adjacent strains or varieties has been proved at several experiment stations. The work of Kiesselbach (1918) at the Nebraska Station is particularly illuminating on this point. Kiesselbach compared competition between adjacent single-row plots and adjacent plots each consisting of from three to five rows. The yield of border rows was in some instances included in the yield of the blocks. His results are summarized in the following table:

TABLE XXIV.—SUMMARY OF RELATIVE GRAIN YIELDS OF VARIETIES TESTED IN SINGLE-ROW PLOTS AND ALSO IN BLOCKS CONTAINING SEVERAL ROWS

Varieties compared in alternating rows and in alternating blocks	Year of test	Ratio of variety 1 to variety 2		
		Alternating rows	Alternating blocks	Competing in same hill
Turkey Red (1) and Big Frame (2) winter wheat.....	1913	100:107	100:97	
Turkey Red (1) and Big Frame (2) winter wheat.....	1914	100:85	100:97	
Turkey Red (1) and Nebraska No. 28 (2) winter wheat.....	1913	100:107	100:107	
Turkey Red (1) and Nebraska No. 28 (2) winter wheat.....	1914	100:63	100:85	
Kherson (1) and Burt (2) oats.....	1913	100:130	100:112	
Kherson (1) and Burt (2) oats.....	1914	100:139	100:101	
Kherson (1) and Swedish Select (2) oats....	1913	100:82	100:77	
Kherson (1) and Swedish Select (2) oats....	1914	100:89	100:93	
Hogue's (1) and Pride of the North (2) corn...	1912	100:66	100:85	100:47
Hogue's (1) and Pride of the North (2) corn...	1914	100:38	100:53	100:26
Hogue's (1) and University No. 3 (2) corn...	1914	100:90	100:98	100:99
Crossbred Hogue's (1) and inbred Hogue's (2) corn.....	1916	100:31	100:37	100:21

¹ Garber and Odland 1926.

A comparison of the columns in Table XXIV, headed "Alternating rows" and "Alternating blocks," show strikingly the effects of competition. In almost every case the varieties grown in alternating rows show a greater difference than the same varieties grown in alternating blocks. Perhaps the extreme effect of competition is shown by different varieties of corn grown in the same hill.

In yield trials for such crops as corn where the hill method of planting is used, variation in stands greatly modifies yield per hill or plot. Studies of Kiesselbach (1923), given in the following table, illustrate this point:

TABLE XXV.—RELATIVE YIELDS OF THREE-PLANT HILLS WHEN ADJACENT TO HILLS WITH VARIOUS NUMBERS OF PLANTS
2-year Average

Three plant hills surrounded by or adjacent to	Total number of hills averaged	Relative grain yield per hill
Surrounded by three plant hills . .	598	100
Adjacent to one hill with two plants	360	102
Adjacent to one hill with one plant	302	107
Adjacent to one blank hill	366	114

If each hill adjacent to a blank hill increased (as it did) its yield 14 per cent, 56 per cent of the loss due to the blank hill would be recovered.

The results presented, together with others of a similar nature, prove that border-effect competition with certain varieties, which result from unequal stands of hill crops and competition between near-by varieties, is a source of error in plot or nursery experiments. Such errors may be controlled by various means, some of which are mentioned here:

1. Similar sorts may be grouped, as is recommended by Love, for yield tests in rod-row trials of small grains.

2. Multiple-row plots may be used and border rows removed, a method frequently used in rod-row tests of small grains conducted in the Great Plains area of the United States.

3. With crops, such as corn or soybeans, surplus seed may be planted and later the rows may be thinned to a uniform stand.

4. For hill crops, such as potatoes and corn, perfect stand hills surrounded on all sides by perfect stands can be harvested for yield trials.

5. For field-plot tests the outside rows can be discarded and yields based upon center rows. In drilled plots of small grains the two outside drill rows and 1 or 2 feet of grain from the end of each plot may be removed before harvest.

After taking all possible precautions to eliminate systematic mistakes, there will remain certain errors which, under field conditions, it is impossi-

ble to avoid. By a statistical analysis the data are studied further for the purpose of learning the probabilities that the differences observed are of real significance and not a result of random sampling. Probable-error methods of comparison may be grouped under three general heads:

1. Computation of probable errors for each individual variety or strain.
2. Computing a probable error of the experiment in percentage which is used to obtain probable errors for any variety or strain in the test.
3. "Student's" method of comparing results.

These and other methods are of relatively recent application and, unfortunately, as yet there are no universally recognized standard means of statistical treatment for field-plot trials. Certain methods now in use will be illustrated and some of their shortcomings mentioned.

Probable Errors for Each Variety.—If four systematically distributed plots are used the probable errors can be computed directly. In this case, $n - 1$ should be used instead of n . This method appears to be the least desirable for a plant breeder. Its undesirability, however, is a subject for debate.

On the basis of a small number of determinations, such as four systematically distributed plots, it may happen by chance that certain varieties may give about the same yield in each of the plots. The calculated probable error in this case will be very small. There is certainly the possibility that all four plots may happen to fall on very productive soil or in places of low productivity. It can be demonstrated that if a single variety is planted on a field and harvested in small plots and if each four plots, systematically distributed, are considered as a separate strain that the computed probable errors may differ by as much as several hundred per cent.

Probable Errors Computed from Checks.—There are various methods for the calculation of a probable error of the experiment. These will be illustrated and the use of such a probable error will be discussed. Probable errors obtained from check plots may be computed and expressed in percentage. It is possible to use sufficient check plots so that the computed probable error of a single determination, *i.e.*, $S. D. \times \pm 0.6745$, may be reliable for the variety in question. By dividing the probable error of a single determination by \sqrt{n} where n equals the number of systematically distributed, replicated plots, the probable error of the method of trial is obtained. This is mathematically correct only when replication reduces variability as rapidly as theoretically expected. The yield of each variety can then be multiplied by the probable error in percentage which will give a probable error in bushels. When sufficient check plots are not available, an average probable error of the experiment can be obtained by some other means in which the results from all varieties are used and the probable error is computed in percentage.

The Pairing Method of Securing a Probable Error.—Under certain conditions, it is impracticable to devote so large a share of the experimental field to check plots. Wood and Stratton (1910) have suggested a means of securing a reliable probable error without the aid of checks. Briefly, their method consists of systematically pairing similarly treated plots and finding their mean yields. The deviation of this mean from the yield of the original plots is expressed in percentage of the mean. The following illustrates the procedure:

Plot arrangement	A'	B'	C'	etc	A''	B''	C''	etc.	A'''	B'''	C'''	etc
Yield per acre	20	22	21	etc	21	23	25	etc.	24	22	23	etc

Now if all A plots are similarly treated, A' would be paired with A'' and A'' with A''' , etc.

In this method the probable error is expressed in percentage of the mean. If the number of pairs is sufficiently great the deviations + and - will yield a normal frequency curve. As in the method of determining the probable error by means of checks, it is desirable to have a large enough number of variants to secure at least an approach to the normal frequency distribution.

TABLE XXVI—THE PAIRING METHOD

Plot	Yield	Mean	Deviation	Deviation in percentage of mean
A'	20	20.5	0.5	2.4
A''	21			
A'''	21			
etc.	24	22.5	1.5	6.7

Similarly, the yields of B', B'', and B''' are paired, etc., as with the A series. After treating all varieties in a similar manner, the average deviation in percentage is obtained. This was used by Wood and Stratton as a probable error in percentage for a single determination.

They (1910) present the following probable errors obtained by the pairing method, based on a large number of replicated plots of wheat, barley, oats, mangels, rutabagas, potatoes, and seed grasses:

400 pairs of plots, different sizes	P. E. 4.2 per cent
45 pairs of plots, each $\frac{1}{2}$ acre.	P. E. 3.5 per cent
52 pairs of plots, each $\frac{1}{4}$ acre.	P. E. 3.5 per cent
29 pairs of plots, each $\frac{1}{20}$ acre.	P. E. 3.9 per cent
200 pairs of plots, each $\frac{1}{40}$ acre.	P. E. 4.6 per cent
75 pairs of plots, each $\frac{1}{80}$ acre.	P. E. 3.1 per cent

In this method the average deviation of plots, systematically paired, is used directly as a probable error. A modification of this method was suggested (Arny and Garber, 1919) by squaring each percentage deviation, summing these squared deviations, dividing the sum by the number of deviations, and extracting the square root of the quotient. This gave a probable error somewhat higher than that obtained by Wood and Stratton. Another method of computation which is called the "deviation from the mean method" has been suggested by Hayes (1923). The latter method gave results more nearly like those obtained from check plots and accordingly its calculation is discussed here in some detail.

The Deviation from the Mean Method.—A plant breeder, in the majority of cases, centers his attention chiefly upon a few characters at a time and discards rather freely. For this reason the strains which are under trial are perhaps not widely different in general adaptability. For several years in the Minnesota-plant breeding studies, a comparison has been made of probable errors calculated by different methods.

Check plots of standard varieties—Marquis wheat, Manchuria (Minn. 184) barley, and Victory oats—have been planted every fifth to tenth plot throughout the rod-row trials and probable errors calculated from these plots¹ have been used as standards for comparison of other methods of obtaining probable errors. Probable errors obtained by the deviation from the mean method and by Wood and Stratton's pairing method were compared with the probable errors obtained by the use of check plots. It was found that the deviation from the mean method gave results which were closer to those obtained from check plots than were the probable errors calculated from the pairing method. Garber and others (1924), at West Virginia, have compared probable errors computed from check plots with those obtained from the deviation from the mean method for a 3-year period for buckwheat and for 2 years for oats and wheat. Agreements were good except for buckwheat. The deviation from the mean method gave a probable error in 1921 twice as great as obtained by the use of check plots. The only other wide variation was in 1923 for wheat studies, the percentage probable error by the check-plot method being 12.9 and by the deviation from the mean method, 18.9.

The computation for the deviation of the mean method where the yields obtained from different varieties are used to calculate a single probable error in percentage may be given as follows:

Computing of Probable Errors by the Deviation from the Mean Method

1. Express in per cent the deviation of each plot of each variety from its variety mean.

¹ The formula used was $P. E. = \pm 0.6745 \sqrt{\frac{\sum(d^2)}{n}}$.

2. Square these percentage deviations and sum by adding all squared deviations.

3. Divide the sum of the squared deviations by the total number of deviations and extract the square root

4. After extracting the square root multiply the value obtained by ± 0.6745 . The value obtained is the probable error of a single plot test in percentage.

5. To compute the probable error of any number of systematically distributed plots, n divide the P. E. of a single plot by the \sqrt{n}

6. Multiply the yield by the percentage probable error to obtain a probable error in bushels.

The method of computation is illustrated here although much larger numbers are desirable than are used in the illustration. With small numbers the squared deviations should be divided by $n - 1$ instead of n . One of the advantages of the plan is that so many deviations are obtained that an accurate estimate of the extent of variability is reached. The plan is illustrated for two varieties each grown in four systematically distributed plots. Commonly, at least 100 deviations are available in plant-breeding studies.

ILLUSTRATION OF METHOD

Variety	Yield each plot in bushels	Mean	Deviation in bushels	Deviation in per cent	Deviation in per cent squared
Marquis \times Iumillo	35.4	..	4.6	11.50	132.25
II-15-44	48.0	40.0	8.0	20.00	400.00
	37.3	.	2.7	6.75	45.56
	39.2	0.8	2.00	4.00
Marquis \times Kanred	35.5	..	2.7	7.07	49.98
II-15-58	44.4	38.2	6.2	16.23	263.41
	37.4		0.8	2.09	4.37
	35.3	..	2.9	7.59	57.61

$$\sqrt{\frac{957.18}{8}} = 10.9 = \text{S. D. single plot in per cent}$$

$$\frac{10.9}{\sqrt{4}} = 5.45 = \text{S. D. in per cent for four systematically distributed plots by the deviation from the mean of the variety method}$$

$$5.45 \times \pm 0.6745 = 3.68, \text{ P. E. in per cent}$$

It is apparent in the illustration given that plot 2 in each variety was in a favorable position and that there is some correlation in yielding ability of neighboring plots.

The criterion of the accuracy of the method is a comparison with probable errors obtained from the yields of check plots of a standard variety where the probable error equals $\pm 0.6745 \sqrt{\frac{\sum (d^2)}{n}}$.

Results obtained from a 6-year comparison of the two methods are presented in the following table:

TABLE XXVII.—PROBABLE ERRORS OF A SINGLE-PLOT TEST AS OBTAINED FROM CHECK PLOTS OF A STANDARD VARIETY AND FROM A COMBINATION OF OTHER VARIETIES IN THE TRIAL

Crop	Year	Check-plot method (single standard variety)			Deviation of mean method (all varieties)		
		Average yield, bushels	Number of plots	P. E., per cent	Average yield, bushels	Number of plots	P. E., per cent
S. wheat.....	1919	20.3	42	11.8	20.0	108	15.2
	1920	25.8	60	10.1	25.0	252	9.6
	1921	18.6	44	10.2	17.8	140	10.2
	1922	35.4	52	9.2	33.8	292	8.6
	1923	30.9	26	5.2	32.2	360	5.7
	1924	26.9	64	9.0	25.7	328	9.9
Average.....	26.3	..	9.3	25.8	...	9.9
Oats.....	1919	56.4	48	7.6	62.3	132	6.1
	1920	80.7	42	9.2	77.1	788	9.4
	1921	50.7	43	7.5	51.8	388	7.9
	1922	115.6	55	4.7	100.6	160	5.1
	1923	61.6	55	7.0	61.0	579	6.1
	1924	59.0	60	10.4	58.3	292	6.7
Average.....	70.7	..	7.7	68.5	..	6.9
Barley.....	1919	41.9	52	9.5	29.7	80	9.2
	1920	49.1	32	10.0	41.5	188	10.1
	1921	30.9	62	10.0	28.1	232	9.6
	1922	60.7	48	11.6	60.4	520	10.1
	1923	56.1	34	7.1	54.1	324	7.5
	1924	42.5	24	7.9	40.8	76	8.6
Average.....	46.9	..	9.4	42.4	...	9.2
W. wheat.....	1924	45.2	24	5.3	45.6	88	5.1

The two methods of computation gave very similar results. The average for the 6-year period where the probable errors in percentage for the check-plot method are given first and for the deviation of the mean method next are as follows: for wheat, 9.3 and 9.9; for oats, 7.7 and 6.9; and for barley, 9.4 and 9.2. The only differences of any magnitude were in 1919 in which case the probable errors by the two methods are 11.8 and 15.2, respectively, for wheat; and in 1924, 10.4 and 6.7 for

oats. Only a single year's comparison is given for winter wheat as in other years winterkilling occurred in spots in the nursery and prevented obtaining probable errors of any significance. Probable errors in percentage obtained by the two methods in the season in which winterkilling was not a factor are 5.3 and 5.1.

"Student". (1926) has pointed out that the correct mathematical formula, if yields of different replicated strains are used, should be as follows: $S. D. = \sqrt{\frac{\sum(d^2)n}{N(n-1)}}$, where n = size of sample, *i.e.*, number of replicates of each variety, and N = total number of deviations. The computation is not very tedious if d is expressed directly in bushels instead of in percentage. A probable error in percentage can be obtained by dividing the probable error in bushels by the average yield of all plots and then multiplying by 100. Such a generalized probable error does not take correlation of near-by plots into account. Richey (1925) has presented a new method of correcting yields by means of the regression relation and presents a formula for computing a generalized probable error of the experiment which gives a much lower probable error than the "deviation of the mean method." He also compares this with a method suggested by "Student" which does away with correlation within each replication series.

Another method which helps to control variability is to plant in the form of a "Latin square." Briefly, this consists of arranging the varieties in the test at random except for certain restrictions. If A , B , C , and D represent the plots of four different varieties, they could be planted in such a manner that each variety appears once in each row and once in each column and in no case in adjacent plots. Otherwise, the planting is at random. In this method, any shape of plot can be used.

ILLUSTRATION OF METHOD

B	C	A	D
D	A	C	B
C	B	D	A
A	D	B	C

A method of computing a probable error for this arrangement of planting was given by Fisher (1925) and discussed by "Student."

Methods of Using Average Probable Errors.—One of the dangers of using a single percentage probable error of the experiment for each variety is apparent. Some varieties vary more than others and their probable error is larger than the probable error for the average of all varieties. In plant-breeding experiments the varieties frequently are similar and for this reason tend to react in a similar manner. The average probable error may aid in selecting an elimination value below which varieties or

strains may be discarded without danger of throwing away a valuable one. This figure is necessarily more or less arbitrary and will depend upon the desired degree of accuracy. The magnitude of the figure which is multiplied by the probable error will also depend somewhat upon the desired amount of elimination. A method which in some cases has been found of use at the Minnesota station is to subtract the product of three times the probable error for the method of test multiplied by $\sqrt{2}$ from the highest or one of the higher yielding strains. The difference gives a figure below which it is considered safe to discard without danger of eliminating the strain with the highest yielding ability. Strains are not discarded, as a rule, on the basis of a single season's trial. If the yield of a strain falls below the elimination figure for 2 or 3 years, it is discarded from further trials.

The average yield of each variety for each crop season may be multiplied by the percentage probable error and a probable error in bushels can be obtained by this means. It is then possible to compare the yields of any two varieties with each other for any particular season.

A probable error of an average of averages is used in some cases. The method now being tried out is illustrated here. A series of smooth-awned barley hybrids have been compared for several years with Manchuria (Minn. 184). Several of these have yielded well. A cross made between a smooth-awned strain and Manchuria, which carries the Minnesota No 445, has given an average yield in rod-row trials for the 6-year period, 1920-1925, inclusive, of 51.8 bushels, while Manchuria (Minn. 184) yielded 49.0. What are the chances that this difference is significant? Probable errors in percentage for this 6-year period are, respectively, 5.1, 4.8, 5.1, 3.8, 4.3, and 3.5 and by the formula $\frac{1}{N}\sqrt{a^2 + b^2 + \dots + n^2}$, as explained in the chapter on biometry, the average probable error for the 6-year period is 1.8. Multiplying the average yield of each of the varieties by this probable error gives a probable error in bushels of 0.9 for each. A comparison of the two varieties is made as follows:

VARIETY	YIELDS, 1920-1925
Manchuria (Minn. 184).....	49.0 \pm 0.9
Smooth-awned hybrid (Minn. 445).....	51.8 \pm 0.9
Difference.....	2.8 \pm 1.3
Difference/P. E.....	2.2

The odds against the occurrence of a deviation as great or greater than this one on the basis of random sampling are 6.26:1. On the basis of random sampling, however, there is as great a chance of Manchuria (Minn. 184) yielding more than the hybrid as of the hybrid yielding more than Manchuria. If the statement, therefore, is made on the basis of the probabilities that the hybrid is a better yielder than Manchuria;

i. e., deviation in one direction—the odds become twice as great +1 as given in the table of probabilities. On this basis the chances that the hybrid is a better yielder than Manchuria are 13 52:1. If it is desired, therefore, when comparing two varieties as *A* and *B*, to make the statement directly regarding the chances that the higher yielding variety, which may be called *A*, is significantly better than *B* the probability tables presented in the chapter on biometry can be used by multiplying the odds by 2 and adding 1, as illustrated in comparing the smooth-awned hybrid with Manchuria.

For the years 1922-1925, Manchuria and the smooth-awned hybrid have been tested likewise by Prof. A. C. Arny in $\frac{1}{10}$ -acre plot trials at University Farm, St. Paul, Minn. The calculated probable errors in percentage obtained were 2.6, 3.9, 1.0, and 4.1, respectively, which are somewhat smaller on an average than those obtained for the rod-row tests. The calculated average probable error was 1.6. The yields in this case were as follows:

VARIETY	YIELD, 1922-1925
Manchuria (Minn 184)	38 9 \pm 0 6
Smooth-awned hybrid (Minn 445)	48 5 \pm 0 8
Difference	9 6 \pm 1 0

In this case the chances are very great that these varieties differ significantly in yielding ability.

During these same four years, the new variety yielded as well as Manchuria at each of the five Minnesota branch stations. It was originally picked out for increase on the basis of its satisfactory performance and probable errors were used as an aid in eliminating a large number of other strains which on the basis of yield appeared less desirable.

It should be kept clearly in mind that the significance of the difference, calculated in the examples given above, is based on deviation in one direction only and, therefore, gives greater odds than when based on deviation in either direction. In general, where it is possible to apply two tests, the more stringent is preferable.

The "Student" Method of Comparing Two Results on a Probable-error Basis.—This method was brought to the attention of American workers by Love (1923, 1924) who said:

The method consists of finding the difference between the two items compared and then the mean difference. From this mean the standard deviation of the several differences is found by the usual formula

$$S. D. = \sqrt{\frac{fd^2}{n}}$$

The ratio of the mean to the standard deviation is designated by "Student" as *Z*.

The following comparison of yielding ability of varieties *A* and *B* will illustrate the method of computation:

<i>A</i>	<i>B</i>	<i>D</i>	<i>D</i> ²
79.6	77.2	-2.4	5.76
49.7	53.5	3.8	14.44
46.5	66.1	19.6	384.16
63.8	65.8	2.0	4.00
42.4	52.4	10.0	100.00
47.7	57.3	9.6	92.16
		<hr/> 6 42.6	<hr/> 6 600.52
		7.1	100.0867

$$\begin{aligned}
 \text{S. D.} &= \sqrt{100.0867 - (7.1)^2} = \\
 &\quad \sqrt{100.0867 - 50.41} = \\
 &\quad \sqrt{49.6767} = 7.0481 \\
 \text{S. D.} &= Z \frac{M}{7.0481} = 1.007
 \end{aligned}$$

Love (1924) has presented tables by means of which it is very easy to determine the odds that a difference is significant. For example for six comparisons and a *Z* of 1.007, the odds that the two varieties are significantly different in yielding ability is approximately 25.5:1.

TABLE XXVIII.—THE CALCULATED ODDS FOR THE *Z* VALUES OF "STUDENT'S" TABLE FOR ESTIMATING THE PROBABILITY THAT THE DIFFERENCE BETWEEN A SERIES OF PAIRED EXPERIMENTS IS SIGNIFICANT
(In Addition to Calculating the Values for *Z* as Given in Student's Table, the Values for the Intermediate Classes Have also Been Calculated)

<i>Z</i>	<i>n</i> = 2	<i>n</i> = 3	<i>n</i> = 4	<i>n</i> = 5	<i>n</i> = 6	<i>n</i> = 7	<i>n</i> = 8	<i>n</i> = 9	<i>n</i> = 10
0.1	1.14	1.22	1.29	1.35	1.40	1.46	1.50	1.55	1.59
0.15	1.21	1.35	1.46	1.56	1.66	1.75	1.83	1.92	2.00
0.2	1.29	1.49	1.66	1.82	1.97	2.12	2.26	2.41	2.55
0.25	1.37	1.64	1.88	2.10	2.32	2.54	2.75	2.97	3.19
0.3	1.46	1.81	2.13	2.44	2.76	3.08	3.41	3.75	4.11
0.35	1.54	1.98	2.40	2.81	3.24	3.68	4.14	4.62	5.13
0.4	1.64	2.18	2.72	3.27	3.85	4.48	5.15	5.88	6.67
0.45	1.73	2.39	3.05	3.75	4.51	5.33	6.24	7.24	8.34
0.5	1.84	2.62	3.44	4.35	5.36	6.50	7.80	9.26	10.9
0.55	1.94	2.85	3.85	4.97	6.25	7.72	9.42	11.4	13.6
0.6	2.05	3.12	4.33	5.75	7.42	9.42	11.8	14.6	18.0
0.65	2.16	3.39	4.82	6.51	8.62	11.2	14.2	17.9	22.5
0.7	2.27	3.69	5.41	7.55	10.2	13.6	17.8	23.1	29.8
0.75	2.39	3.99	5.99	8.55	11.8	16.0	21.4	28.3	37.2
0.8	2.51	4.33	6.70	9.82	14.0	19.5	26.8	36.5	49.3
0.85	2.62	4.66	7.39	11.1	16.1	22.9	32.1	44.5	61.1
0.9	2.75	5.04	8.22	12.7	18.9	27.7	40.0	57.1	81.0
0.95	2.87	5.41	9.04	14.2	21.7	32.4	47.8	69.4	100
1.0	3.00	5.83	10.0	16.2	25.5	39.2	59.2	89.1	132
1.05	3.12	6.24	11.0	18.2	29.1	45.7	70.4	108	163
1.1	3.26	6.69	12.1	20.6	34.0	54.0	87.5	138	216
1.15	3.39	7.13	13.2	22.9	38.7	63.5	103	166	262
1.2	3.52	7.63	14.5	25.9	44.9	75.9	127	212	344
1.25	3.65	8.11	15.7	28.8	50.8	87.5	151	255	416
1.3	3.79	8.64	17.2	32.3	58.5	104	184	322	555
1.35	3.92	9.16	18.6	35.8	66.1	119	216	381	666
1.4	4.07	9.74	20.3	40.0	75.9	142	262	475	908
1.45	4.20	10.3	21.9	44.0	85.2	163	302	555	1110
1.5	4.34	10.9	23.9	49.0	98.0	191	360	713	1428
1.55	4.48	11.5	25.7	53.9	109	216	434	832	1666
1.6	4.62	12.2	27.7	60.0	124	255	525	999	1999
1.65	4.76	12.8	29.8	65.7	138	285	587	1110	2499
1.7	4.91	13.5	32.2	72.5	158	332	713	1428	3332
1.75	5.05	14.2	34.5	79.0	174	369	832	1666	3332
1.8	5.20	14.9	37.0	86.7	199	434	999	1999	3999
1.85	5.34	15.6	39.5	94.2	216	499	1110	2499	4999
1.9	5.49	16.4	42.5	103	243	587	1249	3332	9999
1.95	5.63	17.1	45.1	111	269	624	1428	3332	
2.0	5.78	17.9	48.3	122	302	713	1666	4999	
2.05	5.92	18.7	51.1	132	332	768	1999	3999	
2.1	6.07	19.6	54.9	144	369	908	2499	4999	
2.15	6.21	20.4	58.2	155	399	999	2499	4999	
2.2	6.36	21.3	61.9	168	454	1249	3332	9999	
2.25	6.51	22.1	65.2	181	499	1249	3332		
2.3	6.66	23.1	69.4	199	555	1428	4999		
2.35	6.81	24.0	73.1	212	587	1666	4999		
2.4	6.96	25.0	77.7	232	666	1999	4999		
2.45	7.10	25.9	81.6	249	713	1999	4999		
2.5	7.26	26.9	86.7	269	768	2499	4999		
2.55	7.40	27.9	91.6	285	832	2499	4999		
2.6	7.55	29.0	97.0	302	908	2499	9999		
2.65	7.70	30.1	102.0	322	999	2499			

TABLE XXVIII.—(Continued)

<i>Z</i>	<i>n</i> = 2	<i>n</i> = 3	<i>n</i> = 4	<i>n</i> = 5	<i>n</i> = 6	<i>n</i> = 7	<i>n</i> = 8	<i>n</i> = 9	<i>n</i> = 10
2.7	7.86	31.2	108	356	1110	3332			
2.75	8.00	32.2	113	369	1110	3332			
2.8	8.16	33.4	118	399	1249	4999			
2.85	8.30	34.5	124	416	1249	4999			
2.9	8.46	35.6	131	454	1428	4999			
2.95	8.61	36.7	136	475	1428	4999			
3.0	8.77	37.9	144	525	1666	4999			
3.05	8.91	39.2	151	555	1666	4999			
3.1	9.07	40.5	158	587	1999	9999			
3.15	9.21	41.6	163	587	1999				
3.2	9.37	42.9	171	624	2499				
3.25	9.52	44.0	178	666	2499				
3.3	9.67	45.5	188	713	2499				
3.35	9.82	46.8	195	768	2499				
3.4	9.98	48.3	203	832	3332				
3.45	10.1	49.5	212	832	3332				
3.5	10.3	51.1	221	908	3332				
4.0	11.8	66.1	322	1666	4999				
4.5	13.3	83.0	434	2499	4999				
5.0	14.0	102	624	3332	9999				
5.5	16.5	122	832	4999					
6.0	18.0	146	999	9999					
6.5	19.6	171	1249						
7.0	21.1	199	1666						
7.5	22.7	226	1999						
8.0	24.3	255	2499						
8.5	25.8	293	2499						
9.0	27.4	322	3332						
9.5	28.9	360	3332						
10.0	30.5	399	4999						
15.0	46.2	908	9999						
20.0	61.9	1666							
25.0	77.7	2499							
30.0	93.3	3332							
35.0	109	4999							
40.0	124	4999							
45.0	140	9999							
50.0	153								
60.0	188								
70.0	221								
80.0	249								
90.0	285								
100.0	311								

TABLE XXVIII —(Continued)

Z	n = 11	n = 12	n = 13	n = 14	n = 15	n = 16	n = 17	n = 18	n = 19
0 1	1 64	1 68	1 72	1 76	1 80	1 84	1 88	1 92	1 96
0 15	2 08	2 16	2 24	2 31	2 39	2 47	2 54	2 62	2 69
0 2	2 70	2 84	2 99	3 14	3 29	3 44	3 60	3 75	3 91
0 25	3 41	3 64	3 87	4 11	4 36	4 60	4 86	5 12	5 39
0 3	4 48	4 86	5 27	5 69	6 13	6 59	7 08	7 59	8 12
0 35	5 67	6 24	6 81	7 47	8 15	8 86	9 62	10 4	11 3
0 4	7 53	8 45	9 47	10 6	11 8	13 1	14 5	16 0	17 7
0 45	9 54	10 9	12 3	13 9	15 7	17 7	19 8	22 2	24 8
0 5	12 8	14 9	17 3	20 1	23 3	26 8	30 8	35 4	40 7
0 55	16 2	19 2	22 7	26 7	31 3	36 5	42 7	49 5	57 5
0 6	22 0	26 8	32 4	39 3	47 3	56 8	68 4	81 6	98 0
0 65	27 9	34 6	42 5	52 2	63 9	77 7	95 2	115	140
0 7	38 1	48 5	61 5	77 7	99 0	124	155	195	249
0 75	48 3	62 7	81 0	104	134	171	216	277	356
0 8	66 1	88 3	118	158	207	277	356	475	621
0 85	83 7	114	155	207	277	369	499	666	908
0 9	114	160	226	311	431	587	832	1110	1666
0 95	144	207	293	416	587	832	1110	1666	2499
1 0	195	293	434	624	908	1428	1999	3332	4999
1 05	243	369	555	832	1219	1999	2499	3999	9999
1 1	332	525	832	1219	1999	3332	1999	9999	9999
1 15	416	666	999	1666	2499	3332	1999		
1 2	555	908	1428	2499	3332	1999	9999		
1 25	713	1110	1666	3332	4999	1999			
1 3	999	1666	2499	4999	9999	9999			
1 35	1249	1999	3332	4999					
1 4	1666	3332	4999	9999					
1 45	1999	3332	4999						
1 5	2499	4999	9999						
1 55	2499	4999							
1 6	3332	9999							
1 65	3332								
1 7	4999								
1 75	4999								
1 8	9999								

TABLE XXVIII.—(Continued)

Z	n = 20	n = 21	n = 22	n = 23	n = 24	n = 25	n = 26	n = 27	n = 28	n = 29	n = 30
0.1	2.00	2.03	2.07	2.11	2.15	2.18	2.22	2.26	2.29	2.33	2.37
0.15	2.77	2.84	2.92	2.99	3.07	3.14	3.22	3.30	3.37	3.45	3.52
0.2	4.08	4.24	4.41	4.58	4.76	4.94	5.12	5.31	5.50	5.69	5.90
0.25	5.66	5.94	6.23	6.52	6.83	7.14	7.46	7.79	8.12	8.47	8.82
0.3	8.68	9.27	9.89	10.5	11.2	11.9	12.7	13.5	14.3	15.2	16.1
0.35	12.2	13.1	14.1	15.2	16.3	17.5	18.7	20.1	21.5	23.0	24.5
0.4	19.5	21.5	23.7	26.0	28.6	31.4	34.3	37.8	41.2	45.3	49.3
0.45	27.7	30.7	34.2	38.1	42.1	46.6	51.6	57.1	63.1	69.9	76.5
0.5	46.4	53.1	60.7	69.4	79.0	89.9	102	117	132	151	171
0.55	66.6	77.1	89.1	103	118	136	155	181	207	237	269
0.6	117	140	166	199	237	277	332	399	475	555	666
0.65	168	203	243	302	356	434	525	624	768	908	1110
0.7	302	384	475	624	768	999	1249	1666	1999	2499	3332
0.75	434	555	713	908	1110	1428	1999	2499	3332	3332	4999
0.8	832	1110	1428	1999	2499	3332	4999	9999	9999	9999	9999
0.85	1110	1428	1999	2499	3332	4999	4999	4999			
0.9	1999	2499	3332	4999	9999	9999	9999				
0.95	3332	3332	1999	1999							
1.0	9999	9999	9999	9999							

"Student's" method was devised primarily for small numbers. In its application to varietal trials, this method involves pairing like plots and the use of "Student's" tables for small numbers of replications. There should be a natural basis, moreover, for pairing, *i.e.*, plots may be paired because they are in close proximity to one another or yearly average yields of two varieties may be paired because both varieties have been grown under similar conditions throughout each of several years. In applying the method to varietal trials, it has been used in comparing yearly means. If one variety is consistently a higher yielder, the method brings out these facts. If one variety, however, yields as much as the other 4 years out of 5 but much less the fifth year because of susceptibility to some disease or because of some other cause, this fact will tend to be covered up by applying "Student's" method to the yearly averages. Mathematically, on the basis of random sampling, it might be supposed that in some succeeding year the low yielding variety would greatly exceed the other. Biologically, this may or may not be possible. Using yearly probable errors will bring out certain facts in such a case where "Student's" method applied to yearly averages will not.

In certain cases "Student's" method is a very convenient tool for the field-plot experimentalist. In a comparison of Gopher oats with the local variety conducted in Southern Minnesota in 1925 by R. F. Crim, Extension Agronomist at Minnesota, narrow plots of Gopher were seeded on several farms in a strip in the field and yields obtained from near-by plots. The results are compared by the use of "Student's" method.

County	Yields per bushel		D	D ²
	Local variety	Gopher		
Fillmore .	72 4	78 9	6 5	42 25
	54 0	73 4	19 4	376 36
	78 4	90 4	12 0	144 00
	38 7	59 4	20 7	428 49
	51 8	64 0	12 2	148 84
Watsonwan	97 9	102 9	5 0	25 00
	81 7	110 2	25 5	650 25
	100 7	95 7	-5 0	25 00
	75 1	67 7	-7 7	59 29
	35 7	53 0	17 3	299 29
Brown . .	55 4	70 0	14 6	213 16
	51 0	71 7	23 7	561 69
	49 5	63 2	13 7	187 69
	74 0	74 5	0 5	0 25
	76 0	83 2	7 2	51 84
Le Sueur .	60 9	68 7	7 8	60 84
Redwood . . .	32 4	35 3	2 9	8 41
	32 0	41 5	9 5	90 25
Cottonwood	81 3	92 4	11 1	123 21
			19 196 9	19 3496.11
			10 3631	184 0058
				107 3938
				76 6120

$$S. D. = \sqrt{184\ 0058 - (10\ 3631)^2} =$$

$$\sqrt{184\ 0058 - 107\ 3938} =$$

$$\sqrt{76\ 6120} = 8\ 7528$$

$$\frac{M}{S. D.} = Z = \frac{10.3631}{8.7528} = 1.183 \text{ Odds = very great}$$

The odds that Gopher yielded significantly more than the local variety are very great in this case.

It is apparent from this discussion that each of the methods has its advantages and disadvantages. A correct understanding of these allows the application of the method which appears most desirable for each specific case. No method of statistical analysis takes the place of common sense in the analysis of experimental data, but they are a very valuable aid in an analysis of results.

Climatic Variations.—One other disturbing factor to be considered in conducting plot tests is variation induced by weather conditions. Its

presence is so obvious to anyone who has worked with growing crops that further comment is hardly necessary. In a year of deficient rainfall the varieties best qualified to subsist under a minimum water supply will yield most. Some seasons are better for the growth of early maturing varieties than for late ones. An epidemic of a plant disease like rust may be fostered or hampered by weather conditions. The question arises, how may errors due to this source be overcome? Conducting an experiment over a period of years is the only effective means at the disposal of the investigator. The strain which fluctuates the least from year to year and also gives a high average performance is most valuable for the farmer.

Summary of Field-plot Technic.—1. Soil heterogeneity is universally present in experimental fields although in varying degrees.

2. The extent of soil heterogeneity for any particular field may be studied by the application of the heterogeneity coefficient which expresses the extent to which near-by plots are similar in productivity. By correlating yields of plots at some distance from each other, the extent of systematic variation can be determined. The extent of variability is obtained by analyzing the yield of check plots and is another means of learning the comparative heterogeneity of two or more fields.

3. If the field varies uniformly from one side to the other, check plots may be used to correct yields. In general, the use of checks to correct yields is undesirable. Correcting yields on the basis of the regression equations and the degree of relationship in yielding ability of near-by plots, as a rule, reduces the size of the probable error.

4. The probable error of an experiment may be reduced most effectively by plot replication. Replication, up to a certain number, rapidly reduces the probable error. The number of replications which should be used depends upon the degree of accuracy desired and the heterogeneity of the soil. As a rule, the larger the area of land used the greater the degree of soil variability which must be overcome. On fairly uniform land three or four replications have been found satisfactory for general breeding studies.

5. Increasing plot size is a less valuable method of overcoming soil heterogeneity than replication. The size of plot used and the method of planting is determined to some extent by the nature of the crop. More reliable results can be obtained by using the size of plot which reduces variability to a minimum, considering the number of strains which must be tested and the value of replication. The use of smaller plots under replication may be of more value than a much larger plot if only a single plot is used for each strain.

6. Plants growing on the border of a plot adjacent to an alley or roadway are usually superior to those growing within the plot; hence, if it is desired to secure yields comparable with those which would be secured

under field conditions, the border plants must be discarded. The border should be removed to a depth of at least 1 foot. Different varieties and strains may have unequal ability to utilize the free space along the pathways between plots and, consequently, a second reason arises for discarding the border. For crops which are grown in hills, as with corn or potatoes, it is advantageous to harvest, for the yield trial, perfect stand hills surrounded by perfect stand hills.

7. Competition exists between near-by varieties and strains. The grouping of varieties and strains so that those of similar habits of growth appear side by side removes to a considerable degree the evil effects of competition. The most effective means of overcoming competition is by the use of sufficiently wide borders which are discarded at harvest.

8. After taking precautions to overcome all systematic errors, the use of the probable-error concept as a means of analyzing the results is of material value. The method used will depend upon the nature of the material which is being studied. Probable-error methods do not take the place of a common-sense analysis but are a valuable aid after considering such important questions as the manner of planting, the amount of seed to plant, size of plots and replication, competition, manner of harvesting, curing, and all other questions which have a bearing on the accuracy of the results.

9. Results of field tests vary from year to year because of changing weather conditions, and, for this reason, it is necessary to extend a test over a period of several years. For varietal trials a minimum of three years is recommended.

CHAPTER V

THE MODE OF REPRODUCTION IN RELATION TO BREEDING

General recognition of the stability of inherited factors has served to emphasize the importance of a knowledge of the mode of reproduction of crop plants. If the crop in question is normally self-fertilized, and has been bred carefully, accidental crosses may cause serious mixtures in the variety and thus prohibit its sale as pedigreed seed. With naturally cross-fertilized plants, self-fertilization often has a detrimental effect. A knowledge of the mode of pollination of a crop is therefore an absolute necessity in outlining correct methods of breeding.

Plants may be placed in two major groups according to their mode of reproduction, asexual and sexual.

The asexual group contains those plants which are propagated by grafting, cutting, layering, or other non-sexual method. The chief crop plants belonging to this group are potatoes, sugar cane, and many fruits.

With most crops, asexual propagation is a means of increasing numbers of plants without, in general, expecting a change in hereditary constitution, although, as will be pointed out later, bud sports of economic importance occur occasionally in asexually propagated plants and are of importance, therefore, to the breeder and grower. If such bud sports are sufficiently frequent they must be taken into account in the plan of the breeders. Some plants which are propagated asexually can be grown also from seed and can be bred, therefore, in the same manner as other sexually propagated plants. Most asexually propagated plants, however, are heterozygous.

It is difficult to group crops according to their mode of pollination since different varieties or strains of a single variety may differ markedly in the extent to which self- or cross-pollination occurs and seasonal conditions may modify the results. It is desirable, however, to group certain crops together and the following headings indicate what appear to be the major subdivisions:

1. Naturally self-pollinated.
2. Often cross-pollinated.
3. Naturally cross-pollinated.
4. Dioecious.

NATURALLY SELF-POLLINATED PLANTS

Wheat, barley, oats, tobacco, potatoes, flax, rice, peas, beans, and tomatoes are some of the more important crops belonging to the naturally self-pollinated group.

The flower types are adapted for various degrees of self- or cross-fertilization, but natural crossing takes place in all of them in varying degrees. The plant breeder, however, is chiefly interested in the final result.



FIG. 15—Natural hybrids in wheat. 1. From right to left: Spike of a pure variety produced from a cross of Turkey winter wheat and Wellman's Eife spring wheat. This is a bearded variety with smooth chaff. The progeny of a single plant of this variety gave 48 bearded, smooth chaffed plants and 2 plants with intermediate (tipped awns) and hairy chaff. 2. From right to left: Preston spring wheat; an F_1 natural hybrid with intermediate awns and hairy chaff. The parental varieties from which these natural hybrids were obtained were grown alternately with Haynes Blue Stem the preceding year.

Wheat.¹—The individual florets of wheat and barley are much alike. The envelope of a floret of wheat, for example, consists of the flowering glume, or lemma, and an inner glume, or palea. The sexual organs consist of a pistil with a two-branched, feathery stigma and of three stamens with anthers, all of which are enclosed by the lemma and palea. Opposite the base of the palea are two tiny sac like organs, lodicules. The increase in size of these organs due to water absorption causes the flower to open. This occurs when the stigma is receptive and at this time the elongation of the filaments causes the anthers to protrude from the glumes, when they promptly dehisce. The process of blooming is very rapid and seldom requires more than 20 minutes. Leighty and Hutcheson (1919) state that the opening of the glumes from beginning to completion may not require more than 1 minute, that the anthers may be extruded

¹ Pope has reviewed much of the literature for cereal crops. See *Jour. Am. Soc. Agron.*, Vol. 8, pp. 209-227.

and emptied of their contents within 2 to 3 minutes, and the glumes again become tightly closed at the end of 15 to 20 minutes. Kirchner (1886) states that about one-third of the pollen falls inside the flower. As the pollen is blown around the field by the wind, it is easily seen that natural crossing may sometimes occur.

Investigators differ in their beliefs regarding natural crossing in small grains. DeVries (1906) says, "Wheat, barley and oats are self-fertile and do not mix in the field through cross-pollination." Biffin (1905) states that he has never observed a case of cross-pollination in wheat; while Fruwirth (1909) lists several German breeders who have given instances of natural crosses. Fruwirth says, "Wheat varieties can be cultivated side by side for years without mixing." Nilsson-Ehle (1915), in Sweden, has found that some varieties show a much greater amount of natural crossing than others. Howard and others (1910a), in India, carefully studied natural crossing in wheat for several years and recorded 231 natural crosses. Smith (1912) reported eight natural hybrids in 96 rows of Turkey winter wheat and Saunders (1905) told of a natural hybrid which occurred at Ottawa. During the last few years at University Farm, St. Paul, at least 2 to 3 per cent of natural crossing in wheat has occurred in the plant-breeding plots. Cutler (1919) mentions frequent natural crosses at Saskatoon, Canada. Garber and Quisenberry (1923) concluded that in 1921 natural crossing occurred in winter wheat grown in experimental plots near Morgantown, W. Va., to the extent of less than 1 per cent. Percival (1921) concludes that many so-called sports in wheat originated as natural hybrids.

Barley.—Barley frequently is self-fertilized while the spike is in the sheath. In some varieties of six-rowed barley the lateral rows overlap in such a way as to form a single row instead of two rows at each edge of the rachis, as in the other six-rowed varieties. Fruwirth (1909) observed natural crosses in six-rowed barleys and concluded there was practically no crossing in six-rowed forms. He records the observations of Rimpau, who noted only eight suspected natural crosses in barley after growing 40 varieties side by side for a period of eight years. Harlan, after several years' observation at University Farm, Minn., noted only two or three natural crosses. Barley probably, therefore, crosses much less frequently than does wheat.

Oats.—The form of the individual flower of oats is very similar to that of wheat and barley. Tschermak (1901) reports four natural crosses observed by Rimpau, and Fruwirth (1909) records five or six crosses observed by Rimpau after cultivating 19 varieties side by side for eight years. A natural cross between a variety of *Avena sterilis* and *A. nuda* was noted by Pridham in 1916.

Results of recent experiments by Stanton and Coffman (1924) give accurate information as to the amount of crossing which occurred

in 1922 between varieties of oats grown in adjacent row plots at Akron, Colo. They grew black- and white-grained varieties in alternate rows and made a determination of the percentage of natural crossing where white-grained plants were the mother variety and where they were naturally pollinated with pollen from black varieties. It was found that varieties differed considerably in this respect as the number of aberrant types which were found in Iowa as a result of natural crossing was 0.97 per cent, while the aberrant types in three other varieties varied from 0.10 to 0.33 per cent. Stanton and Coffman mentioned the fact that Livermore, of Cornell University, conducted a similar test at Ithaca, N. Y. His results indicated that natural crossing did occur but the actual extent of its occurrence was not determined.

Griffie and Hayes (1925) studied natural crossing in oats at University Farm, St. Paul, Minn., by growing black- and white-grained varieties, which flowered at approximately the same time, in alternate rows. The extent of natural crossing for the years 1921 and 1922 varied with the variety. The percentage of aberrant types ranged from 0.04 per cent in Victory to 1.4 per cent in Kanota. It appears reasonable to conclude that natural crossing is at least twice as great as indicated by the off types which were observed. The extent of crossing in Kanota is sufficient to emphasize the necessity of roguing varieties grown in adjacent plots if they are to be kept pure.

Tobacco.—In the tobacco plant the flowers are frequently visited by insects and some natural crossing doubtless takes place. As a rule, only one variety of tobacco is grown in a locality. Howard and others (1910b, c), in India, concluded that there is between 2 and 3 per cent crossing in tobacco. They emphasize the necessity of producing artificially self-fertilized seed. In breeding experiments, artificially selfed seed is generally used and, therefore, few records regarding the degree of cross-pollination are available. As it is so easy artificially to self-pollinate tobacco and as each flower produces many seeds (98,910 seeds per plant; Jenkins, 1914) the amount of natural cross-pollination is of little breeding importance.

✓ **Rice.**—In rice the inflorescence is a terminal panicle of perfect flowers. The one-flowered spikelet has a branched stigma and six stamens. The lodicules are strongly developed. Fruwirth (1909) observed the period of blooming in rice and found that 30 seconds elapsed from the time one flower began to open until it was fully open. Dehiscence of the anthers occurred about 7 minutes later and the flower closed 3 hours afterwards.

Jones (1924) has reviewed the literature of the time of blooming of rice flowers. In some countries blooming occurs before 10 a.m., while in California, Jones noted that three-fourths of the rice flowers observed bloomed between 12 m. and 2 p.m. and a greater proportion of the flowers bloomed between 2 and 4 p.m. than before 12 m.

In rice, self-pollination is the usual method, although opportunities for crossing occur. Hector (1913) thinks crosses may occur at a distance of not more than 2 feet by the agency of the wind. In lower Bengal 4 per cent of crossing was estimated. Ikeno (1914) observed no cases of xenia in 15,000 kernels from 190 families which were examined, although adjacent rows were planted to such varieties that the immediate effects of cross-pollination could be observed. When common rice seeds are treated with iodine, the starch grains are stained blue while glutinous rice shows a red color when similarly treated. Xenia occurs, blue color being dominant over red, when glutinous rice is pollinated by common and the iodine test applied. Fifteen thousand kernels from 190 panicles were examined and no Xenia was found. Thompstone (1915), in upper Burma, finds that pollination usually occurs before the glumes open; however, hybrids were frequently observed in fields of ordinary rice. Parnell and others (1917) observed the amount of natural crossing in pure green plants surrounded by others which possessed seed with a purple tip. A total progeny of nearly 15,000 plants grown from seed produced by the green plants were observed, more than 2,000 plants being studied in each of five different families. The percentage of crossing varied from 0.1 per cent in one variety to 2.9 per cent in another. Alkemine (1914) states that cross-pollination occurs if the anthers, on account of unfavorable environmental conditions, do not assume their natural position. This happens when the stigmas protrude from the glumes and take a pendent position before anther dehiscence takes place. Suzuta and Tomura (1925) observed 0.9 to 1.45 per cent of hybrids in varieties of lowland rice grown in adjacent rows.

Peas and Beans.—Piper (1912) finds that natural crossing in the cowpea occurs but rarely in most localities. At Arlington Farm, in the experimental plots, instances of natural crossing have been observed. In some instances, natural crossing occurs more frequently. Thus, an Indiana farmer, who originally grew only eight varieties, found after several years that he had over 40 types. The new types, Piper concluded, were the result of natural crosses. Similar crosses have been observed at the Michigan Station. Harland (1919) has recorded a supposed case of a natural cross which occurred in one of his hybrid cowpea families.

Natural hybrids of soybeans have been observed at the United States Experimental Farm in Virginia and also at the Kansas Experiment Station (Piper, 1916). They were detected by the peculiar color of their seed. Woodworth (1922), by alternating plants of different varieties, concluded that there was 0.16 per cent of natural crossing in the soybean varieties studied. At the West Virginia experiment station (Garber and Odland, 1926) the extent of natural crossing which produced contamination between varieties grown in rows 30 inches apart was 0.14 of 1 per cent in 1922 and 0.36 of 1 per cent in 1923.

Although horticultural peas and beans are largely self-pollinated, cross-pollination does occasionally occur. Howard and others (1910a) give observations in India which indicate natural crosses both in garden and field peas.

Tomatoes.—Jones (1916) planted alternate plants of dwarf and standard varieties of tomatoes 3 feet apart in a field. Seed from the dwarfs was tested the following year. As standard habit is a dominant character, pollen from a standard plant fertilizing a dwarf would give a standard in F_1 .

A total of 2,170 plants were grown from seed of dwarfs and 43 proved to be standards. This is practically 2 per cent. As there was nearly as great opportunity for dwarfs to be crossed with dwarf pollen, it would seem that between 3 and 4 per cent of crossing occurred in this experiment.

Lesley (1924) in a similar experiment conducted at the Citrus Experiment Station, Riverside, Calif., obtained 4.9 per cent cross-fertilization for the variety Magnus and 0.59 per cent for Dwarf Champion. He concluded that there was a varietal difference.

OFTEN CROSS-POLLINATED PLANTS

Certain crops, as has been noted, are usually self-pollinated and other crops are normally cross-pollinated. There are, however, numerous crops in which there is a relatively high percentage of self-pollination and in which cross-pollination is also rather frequent. These crops can be bred in the same manner as self-fertilized crops but some method of isolation must be used to insure self-pollination. The most important crops which are discussed here are grain sorghums, cotton, alfalfa, white sweet clover, and certain of the grasses.

Grain Sorghums.—Ball (1910) states:

All sorghums are adapted to open or wind pollination and most of them are probably adapted to self-fertilization. In adjacent rows of different varieties flowering on approximately the same date, as high as 50 per cent of the seed produced by the leeward row was found to be cross-pollinated. It is probable that in a fairly uniform field of any given variety a similar percentage of natural crossing takes place.

Graham (1916), in India, made a careful study of the amount of cross-fertilization in the Juar plant (*Andropogon sorghum* Brot.). Crossing was more frequent in the looser types of inflorescence than in the compact types. Single-plant cultures were used for the study, which extended over a period of 7 years. The percentage of crossing obtained by counting a given number of plants and noting those which were untrue to type gave 97 plants out of 1,577 (6 per cent) in the loose-headed type and only two plants out of 292 (0.6 per cent) in the compact type of

panicle. Preliminary studies were made by Karper and Conner (1919) of the amount of cross-pollination in plants of white milo which were found growing in a plot of yellow milo. The yellow and white varieties flowered simultaneously. Forty-one heads of white milo which had been surrounded by yellow milo were planted the following year. An average of 6 per cent of natural crossing in plants so surrounded was noted.

Sieglinger (1921) observed the extent of cross-pollination at the Woodward Field Station, in 1919, between adjoining rows of standard yellow and standard white milo. The two varieties differ only in seed color. The progeny of the white milo plants were grown and 276 yellow-seeded plants were observed in a total of 5,125 which indicated 5.38 per cent of the white milo was fertilized by pollen of the yellow-seeded variety. Swanson (1923) studied the frequency of cross-pollination in the F_2 generation of crosses of *feterita* \times Red Amber in which segregation for midvein color was obtained. White midvein is dominant to dull grey and one factor difference is involved. Grey midvein plants should breed true in F_3 if self-pollination is the rule. An F_3 progeny of grey midvein F_2 plants was studied and 2,816 produced grey midveins and 597 produced white midveins. Thus 17.48 per cent of the plants were off types and resulted from cross-pollination.

Cotton.—Because of the rather wide differences in the frequency of cross-pollination observed by different investigators, it appears that varietal differences are one probable cause for the discrepancies.

Leake (1911) observed 5 per cent of natural crossing in India; Webber, as a result of studies in southeastern states, concluded that ordinarily 5 to 10 per cent of the seeds are the result of cross-pollination; while Balls (1912) found that in a field of Egyptian cotton 6 to 10 per cent of plants which resulted from cross-fertilization were obtained.

Kearney (1923) has reviewed much of the literature of the extent of natural cross-pollination in cotton and has presented new evidence. He says:

The three principal types of cotton grown in the United States, upland, sea island, and Egyptian, although very different in their botanical characters, intercross readily.

Kearney finds that when two varieties are grown in close proximity and where pollinating insects are abundant, that the proportion of natural hybrids seldom exceeds 20 per cent and is often much lower. Upland cotton produces more natural hybrids than Egyptian.

Alfalfa.—Piper and others (1914) working with alfalfa have found about the same percentages of seed set when a flower was self-pollinated as when it was crossed with pollen from flowers on the same plant. When cross-pollination was practiced, approximately 50 per cent more seed was obtained than from self-fertilization. They also found that pollen of

Medicago falcata was as efficient in fertilizing *M. sativa* as pollen from other *sativa* plants

Waldron (1919), in North Dakota, planted together in equal numbers two species of *Medicago*, *sativa* and *falcata*. Seeds from each of the species were planted the following year and the number of hybrids noted. From *M. falcata* 42.7 per cent of hybrid plants were obtained and from the *M. sativa* seed about 7.5 per cent. A part of the difference in the results is doubtless due to the fact that the *falcata* plants produce a smaller number of flowers and are procumbent to prostrate in habit.

White Sweet Clover, *Melilotus Alba*.—There is some difference of opinion regarding the extent of cross- and self-fertilization in white sweet clover. Coe and Martin (1920) state that Kirchner and Kerner find that self-pollination generally occurs and that cross-pollination is not necessary for the production of seed. In experiments performed by Coe and Martin, individual racemes were covered with cheesecloth to protect them from insect pollination and seed setting was compared with unprotected racemes. The studies were carried on at Ames, Iowa, and Arlington, Va., and in both cases the percentages of flowers that set seed were very low on covered racemes, averaging 2.9 per cent, while 66.51 per cent of the flowers of unprotected racemes set seed.

Elders (1925) carried on a similar study at University Farm, St. Paul, Minn. The racemes were covered with parchment paper bags and seed setting compared with that on uncovered racemes. White sweet clover set seed readily under these conditions. Kirk (1925b) enclosed racemes of white sweet clover in cotton cages. He obtained an average of 34.91 pods per raceme when enclosed in cages as compared with 66.43 pods per raceme for open-pollinated plants. Kirk says:

Melilotus alba is highly self-fertile and will set seed freely without the visitation of insects. Self-fertilization may be the rule, but not necessarily so, under field conditions in Saskatchewan.

Grasses.—Certain of the grasses are highly self-fertile under conditions of isolation while other grasses are self-sterile or partially so. As little data are available by which to determine the extent of cross- or self-fertilization under normal field conditions, it seems best to treat all grasses considered at one time.

Certain of the crops discussed in the naturally cross-pollinated group may belong to the naturally selfed or often cross-pollinated group.

NATURALLY CROSS-POLLINATED PLANTS

Maize.—Maize has been placed at the head of the cross-pollinated group, as crossing is its normal form of reproduction. Pruwirth (1909) found a setting of 24 per cent in unenclosed corn plants when far enough

from other plants to prevent crossing. Knuth (1909), in similar experiments, found 16 per cent selfing on the upper ear and 4 per cent on the lower. Preliminary experiments have been made by planting corn with a recessive endosperm color in a field of a variety with a dominant endosperm character. Self-fertilization in these experiments was probably less than 5 per cent (Waller, 1917; Hayes, 1918b).

Kiesselbach (1922) conducted careful studies of the extent of cross-pollination of 40 plants of white dent distributed in a field of yellow dent. Only 0.7 per cent of the kernels were actually selfed under natural field conditions.

Rye.—The flowers of rye are very similar to those of wheat and barley. According to Hildebrand the anthers project between the partly closed glumes until the bases protrude. They then tip over and dehisce, spilling part of the pollen outside the flower. Being lower than the stigma the pollen cannot reach the stigma of the same flower. There is some evidence (Ulrich, 1902; Fruwirth, 1909) which indicates that the rye flower is self-sterile, but that the spikelet is not necessarily so. Studies by Brewbaker prove that one individual floret can produce seed when self-fertilized.

Heribert Nilsson (1916, 1919) isolated lines of Petkuser which were highly self-sterile. Approximately 1 or 2 lines out of every 100 tested proved self-fertile.

A waxless rye, which can be easily distinguished from normal rye by the bright-green color of the leaves and stem and which behaves as a simple Mendelian recessive to normal, was used as an indicator of the extent of cross-pollination. Single waxless plants planted at a distance of approximately 60 meters from a 3,500-square meter plot of normal rye showed vicinism to the extent of 54.4 per cent while a plot of twenty waxless plants at the same distance from the plot of normal plants were cross-pollinated to an extent of 37.3 per cent.

Clovers.—It has been pointed out that white sweet clover, *Melilotus alba*, sets seed freely under conditions of self-pollination. Elders (1925) and Kirk (1925) find that yellow sweet clover, *Melilotus officinalis*, set very little seed in racemes enclosed in cotton or parchment covers and Elders found that Hubam sweet clover, *Melilotus alba annua*, reacted in a similar manner to yellow sweet clover.

Fergus (1922) and Kirk (1925a) artificially self-pollinated heads of red clover. The method consisted of bagging the heads singly, just as the petals were beginning to show. After 48 to 60 hours the bags were removed and heads rolled gently between the thumb and fingers. The conclusion was reached that some lines were highly self-fertile. Williams (1925) believes red clover to be self-fertile to a slight extent and agrees with Fergus and Kirk that the degree of self-sterility varies with different plants. Williams, however, concludes that owing to the small

amount of seed set under conditions of self-pollination that the method is not practical for the breeder of red clover.

Sunflowers.—It was believed formerly that sunflowers were self-sterile. Hamilton (1926) reports that some strains are highly self-fertile although the extent of cross- or self-fertilization under normal conditions is unknown.

Grasses.—Some studies with grasses have been reported by Frandsen (1917). Results obtained are given in Table XXIX. Some sterility is indicated by comparing the results of self-fertilization with those of cross-fertilization and natural pollination. *Poa fertilis* and *Bromus arvensis* appear self-fertile. Considerable self-sterility is indicated in orchard grass, timothy, and fescue.

TABLE XXIX.—POLLINATION OF GRASSES

Common name	Scientific name	Percentage seed setting		
		Self-fertilizing	Cross-fertilizing	Free-flowering
Orchard	<i>Dactylis glomerata</i>	1 3-11 5	4 3-75 8	50 0
Tall meadow oat	<i>Arrhenatherum elatius</i>	5.4- 9 4	47 9	51 0
Fescue	<i>Festuca pratensis</i>	3 6- 9 2	17.8-54 0	35 2-47 7
Meadow foxtail	<i>Alopecurus pratensis</i>	7 0-23 3	29 0-69.5	73 2
Italian rye	<i>Lolium multiflorum</i>	10 3	79.8
Timothy	<i>Phleum pratensis</i>	0 8- 8 5	52 0	91 3
	<i>Poa fertilis</i>	59.7-66 8	63 5-65 5	70 4
Brome	<i>Bromus arvensis</i>	66 6-80.0	80 4	77 2-89 2

For several years pollination studies have been conducted at University Farm, St. Paul, Minn., with several grasses. The work was originally undertaken by a graduate student who started the study at Winnipeg under the direction of Prof. W. Southworth. The percentage of seed setting is presented in the following table:

TABLE XXX.—COMPARISON OF SEED SETTING IN CAGES AND OF THE SAME PLANT WHEN EXPOSED

Grasses	Seed set per panicle	
	Bagged	Exposed
<i>Agropyron tenerum</i> (slender wheat)	34.28	55 61
<i>Dactylis glomerata</i> (orchard)	22.83	93.28
<i>Festuca pratensis</i> (meadow fescue)	13 04	64 54
<i>Agrostis stolonifera</i> (red top)	145.58	524 92
<i>Bromus inermis</i> (brome)	5.25	61.04

During the years 1923 to 1925, inclusive, grasses were started in the greenhouse and individual plants isolated by space isolation in the small

1925
MAY 19

grain nursery. Seed setting was compared with that obtained from plots consisting of several plants. The plan was changed in 1924 and individual plants of both high and low seed-setting lines were selected.

TABLE XXXI.—COMPARISON OF SEED SETTING UNDER SELF-FERTILIZATION (BY ISOLATION) AND UNDER CROSS-POLLINATION CONDITIONS

Species	Percentage seed setting		Percentage seed setting, 1925, isolated				Exposed
			High line		Low line		
	Per cent setting 1924 parent	Per cent progeny	Per cent setting 1924 parent	Per cent progeny			
					Isolated	Exposed	
<i>Agropyron tenerum</i>	51.8	51.8	66.0	59.2	33.0	55.9	57.7
<i>Dactylis glomerata</i>	6.1	28.7	7.0	19.7	0.5	14.5	6.1
<i>Festuca pratensis</i>	2.3	16.2	5.3	11.8	0.2	0.6	16.8
<i>Agrostis stolonifera</i>	4.8	38.7	21.0	1.3	0.4	0.8	0.8
<i>Bromus inermis</i>	15.4	34.7	61.0	6.0	1.1	1.5	2.4

The numbers of plants used were small, approximately six plants for each group being used each year. *Agropyron tenerum* appears self-fertile and there is some indication that lines differing in ability to set seed can be isolated in the other grasses.

With timothy, sufficient seed is obtained from heads enclosed in parchment paper bags so that self-fertilization can be used in breeding work. Some lines, however, are highly self-sterile and others highly self-fertile (Hayes and Barker, 1922; Hayes and Clark, 1925).

DIOECIOUS PLANTS

Some of the most important dioecious plants are hops, hemp, date palm, spinach, and asparagus. These plants are always cross-pollinated and may be handled by the breeder in the same manner as self-sterile plants of the cross-pollinated group.

EFFECTS OF A CROSS IN NORMALLY SELF-FERTILIZED SPECIES

A cross between closely related varieties frequently exhibits a quite marked increase in vigor when compared with the parents. This is a manifestation of the same phenomenon as decrease in vigor which is commonly the result of self-fertilizing a naturally cross-fertilized species. With self-fertilized crops it is usually not possible to utilize this increased vigor because the cost of producing crossed seed is too great. Examples of F_1 crosses in tomato, tobacco, and wheat will be given.

Table XXXII gives the comparative yields of first generation tobacco crosses and their parents. All crosses do not prove equally vigorous and a few give no increase as compared with the parental average. In general, however, the crosses show increased yields. As the tobacco flower produces many seeds, Houser (1912) believes the extra cost of production would not be prohibitive. Before this plan can be adopted commercially,

extensive studies are needed to determine the value of particular F_1 tobacco crosses.

TABLE XXXII.—RELATION OF YIELD PER ACRE BETWEEN FIRST GENERATION HYBRID TOBACCO AND THE PARENT PLANTS

Average yield of parents, pounds	Average increase of hybrid over parents, pounds	Maximum increase of hybrid over parents, pounds
800- 900	260	485
901-1,000	212	464
1,001-1,100	185	354
1,101-1,200	153	315
1,201-1,300	153	285
1,301-1,400	159	239
over 1,400	156	189

Difference in yield of parents	Average increase of hybrid over parents, pounds	Maximum increase of hybrid over parents, pounds
1- 100	197	485
101-200	131	181
201-300	189	260
301- 400	97	360
401-500	164	215
over 500	175	465

The vigor of F_1 tomato crosses has received some study. The first extensive test was made by Wellington (1912) at the Geneva (New York) Station. A 3-year test was made under field conditions of a cross between Dwarf Aristocrat, a dwarf tomato, and Livingston Stone. Yields of the parents, the F_1 , and the F_2 generations, are given.

TABLE XXXIII.—YIELDS OF FRUIT IN THE F_1 AND F_2 GENERATIONS OF A CROSS BETWEEN DWARF ARISTOCRAT AND LIVINGSTON STONE WITH THE PARENTS

Data taken	Year	Dwarf Aristocrat, pounds	Livingston Stone, pounds	F_1 , pounds	F_2 , pounds
Ripe fruit per plant.	1908	8.5	12 3	13 9	
Ripe fruit per plant.	1909	6 1	10 1	12.9	12 0
Ripe fruit per plant.	1910	7 0	12 0	13 2	10 0
Average	7 2	11.5	13 3	11 0
Total fruit per plant.	1908	14.8	20 9	25 3	
Total fruit per plant.	1909	9.7	17.7	20 0	20 0
Total fruit per plant.	1910	14.8	24.7	27 7	25.1
Average.	13.1	21.1	24 3	22.6

Not so much interest is placed at the present time in the commercial value of such crosses as in the development of the principle involved.

Wellington believes the above cross of sufficient value to more than pay for the cost of producing crossed seed.

Similar results were obtained at the Connecticut Station in a cross between Stone and Dwarf Champion tomatoes. The experiment was carried on for 4 years (Hayes and Jones, 1916). The lowest increase in yield over the better parent was 11 per cent and the highest 17 per cent. The cross averaged 15 per cent more fruit by weight than the better parent.

In average weight of fruit, the cross exceeded the parental average by 8 per cent. It approached the fruit number of the Dwarf Champion parent and exceeded the average fruit number of the parents by 8 per cent. The cross also matured somewhat earlier than the early parent. A cross between the standard varieties, Lorillard and Best of All, was also studied. The parents produced about the same average size and weight of fruit and the cross about the same as the parents.

A determination of the comparative vigor of F_1 wheat crosses and their parents was made by Fred Griffiee (1921). For this purpose pure lines of *T. durum*, *T. dicoccum*, and *T. compactum* were crossed with pure-line varieties of *T. vulgare*. Intervarietal crosses between pure lines of *T. vulgare* were also studied, as well as crosses between *T. compactum* with *T. durum* and *T. dicoccum*.

A determination of the immediate effect of foreign pollen on size of seed was made. Parental plants were emasculated and then some of the spikes were artificially pollinated with pollen from other plants of the same pure line (incrossed seed) and, in another series, spikes were pollinated with pollen from another variety or species (crossed seed). Only those crosses were compared in which the average date of pollination was about the same for the incrossed and crossed seed. Results are presented in the following table:

TABLE XXXIV.—WEIGHT OF SEED OF INCROSSED PARENTS COMPARED WITH WEIGHT OF THE IMMEDIATE CROSS

Name of cross	♀ Parent		Cross		Difference cross-female parent
	Number of seeds	Average weight seed, milligrams	Number of seeds	Average weight seed, milligrams	
Marquis × Velvet Chaff...	38	12.6 ± 0.5	48	15.6 ± 0.5	+3.0 ± 0.7
Marquis × Penny.....	38	12.6 ± 0.5	24	20.2 ± 1.0	+7.6 ± 1.1
Haynes Bluestem × Marquis.....	49	17.2 ± 0.8	26	23.5 ± 0.7	+6.3 ± 1.1
Little Club × Marquis...	39	10.1 ± 0.5	50	9.4 ± 0.3	-0.7 ± 0.6
Emmer × Velvet Chaff...	44	26.4 ± 0.8	24	27.1 ± 1.3	+0.7 ± 1.5
Velvet Chaff × Mindum...	104	19.9 ± 0.6	23	15.9 ± 0.6	-4.0 ± 0.8
Emmer × Little Club....	44	26.4 ± 0.8	15	25.0 ± 1.2	-1.4 ± 1.4

All three crosses between varieties of *T. vulgare* gave increases over incrossed seed. These appear significant in relation to the computed probable errors. Of the crosses between wheat species only one gave a difference which appears at all significant. In the cross between Velvet Chaff and Mindum the incrossed seed seems somewhat heavier in the light of the probable error than the crossed seed. These results show an immediate effect of pollination on seed size in crosses between varieties of *T. vulgare*.

The emasculation and artificial pollination causes a reduction in seed size as compared with normally produced seed. Incrossed, normally produced seed and crossed seed were grown in the greenhouse under controlled conditions and the comparative vigor of parents and crosses was determined. As there were no significant correlations between size of seed planted (even when incrossed seed was compared with normal seed) and resultant plant vigor, the differences between the parents and crosses may be explained on the basis of inheritance.

Average yield of plants in grams of seed will be used as a measure of vigor (see Table XXXV).

TABLE XXXV --AVERAGE YIELD PER PLANT OF F_1 WHEAT CROSSES AND THEIR PARENTS

Name of one parent	Number of individuals	Yield, grams	Name of other parent	Number of individuals	Yield, grams	Average weight parents, grams	Cross	
							Number of individuals	Yield, grams
Marquis	15	1.9	Penny	36	2.1	2.2	18	2.7
Marquis	15	1.9	Bobs	59	3.0	2.5	65	3.3
Velvet Chaff	38	1.5	Penny	36	2.1	2.0	28	2.5
Velvet Chaff	38	1.5	Bobs	59	3.0	2.3	92	2.9
Penny	36	2.4	Bobs	59	3.0	2.7	23	2.8
Haynes Bluestem	17	2.1	Marquis	15	1.9	2.2	18	2.5
Marquis	15	1.9	Little Club	46	2.2	2.1	45	2.3
Velvet Chaff	38	1.5	Little Club	46	2.2	1.9	37	2.5
Average	30	1.9		45	2.5	2.2	41	2.7
Little Club	46	2.2	Emmer	48	1.1	1.7	9	0.3
Little Club	46	2.2	Mindum	49	2.1	2.2	1	1.0
Marquis	15	1.9	Mindum	49	2.1	2.0	13	0.3
Velvet Chaff	38	1.5	Mindum	49	2.1	1.8	8	1.1
Velvet Chaff	38	1.5	Emmer	48	1.1	1.3	23	0.5
Marquis	15	1.9	Emmer	48	1.1	1.5	18	0.6
Average	33	1.9		49	1.6	1.8	12	0.6

The crosses between varieties of *T. vulgare* and the crosses between *T. vulgare* and *T. compactum* gave in every case slightly greater yields per plant than the average of the parents. On the other hand, F_1 crosses between durum or emmer varieties and varieties of common or club wheats were all significantly lower in yield than the parents. The low yields of these species crosses are due in a large measure to sterility for

there was an appreciably smaller setting of seeds in the crosses than in their parents.

Crosses between distinct species of self-fertilized plants have been carefully studied in the tobacco genus; *Nicotiana*. Results obtained may be summed up as follows (East and Hayes, 1912):

(a) plants so different that they will not cross; (b) crosses that produce seed that contain no proper embryo; (c) crosses that produce seed with embryo, but which go no further than the resting stage of the seed; (d) crosses less vigorous than either parent; (e) crosses more vigorous than the average of the parents; and (f) crosses more vigorous than either parent.

Apparently in wide crosses the normal physiological processes are interfered with. The statement is frequently made that this is due to lack of compatibility between the parents. Incompatibility is correlated apparently with differences in hereditary qualities which are in turn dependent upon differences in numbers or quality of chromosomes or both.

EFFECTS OF ARTIFICIAL SELF-FERTILIZATION AND CROSS-FERTILIZATION IN OFTEN CROSS-POLLINATED PLANTS

The F_1 crosses between sorghums of the various classes, such as kafirs, milos, or feteritas, were found to exhibit extraordinary hybrid vigor, while crosses within a class, *i.e.*, an F_1 cross between two varieties of milo, showed little or no hybrid vigor (Conner and Karper, 1923). The same writers (1924) found that kafir could be inbred for many years without loss of vigor which they state gives the breeder of sorghums an unusual opportunity to establish and distribute highly productive lines. Kearney (1923) has presented similar results for Pima cotton. Strict inbreeding by artificial self-fertilization during five to seven generations caused no reduction in vigor. Kearney says:

The inbred families were not inferior to the continuously open-pollinated stocks in viability of the pollen; number of ovules; daily flower production; percentage of bolls retained; size, weight, and seed content of the bolls; weight and viability of the seeds; and abundance of fiber.

From these conclusions it appears that members of the "often cross-pollinated group" can be bred in the same manner as self-fertilized crops except that some method of controlling cross-pollination and insuring self-fertilization must be used.

EFFECTS OF SELF-FERTILIZATION IN NORMALLY CROSS-FERTILIZED PLANTS

This subject will be studied in relation to the specific outline for breeding some normally cross-fertilized plants, such as maize and rye. A few data will be presented in order to illustrate the general results. The

theoretical explanation is given, as an appreciation of these phenomena is essential in obtaining a correct plant-breeding perspective.

The most extensive studies made have been those with maize. As this crop is almost entirely cross-pollinated under natural field conditions it is an admirable one to contrast with self-fertilized plants. Table XXXVI presents differences in yield and height obtained at the Connecticut Station with four self-fertilized strains of Leaming Dent. These strains were grown only in small plots, therefore differences are only indicative of the general results which may be expected. Crosses between individual plants within a strain that had been selfed 6 or 7 years, were not appreciably more vigorous than the progeny of self-fertilized seed. These strains also differ in other characters, such as shape of ear, width of leaf, and color in various organs. One strain of Leaming Dent No. 1-12 was self-fertilized for about 7 years. It produced well-developed tassels but few ears and was eventually lost.

TABLE XXXVI.—THE EFFECT OF INBREEDING ON THE YIELD AND HEIGHT OF MAIZE

Year grown	Number of generations selfed	The four strains							
		1-6-1-3, etc		1-7-1-1, etc		1-7-1-2, etc		1-9-1-2, etc.	
		Yield, bushels per acre	Height, inches	Yield, bushels per acre	Height, inches	Yield, bushels per acre	Height, inches	Yield, bushels per acre	Height, inches
1916	0	71.7	117.3	74.7	117.3	74.7	117.3	71.7	117.3
1905	0	88.0		88.0		88.0		88.0	
1906	1	59.1		60.0		60.9		12.3	
				1907		1907			
1908	2	95.2		59.3		59.3		51.7	
				1908		1908			
1909	3	57.9		46.0		59.7		35.4	
1910	4	80.0		63.2		68.1		47.7	
1911	5	27.7	86.7	25.4	81.1	11.3	90.5	26.0	76.5
								1913	
1912	6	38.9	
								1914	
1913	7	41.8	.	39.4	45.4	85.0
								1915	
1914	8	78.8	96.0	47.2	83.5	58.5	88.0	21.6	
								1916	
1915	9	25.5	...	21.8	30.6	78.7
								1917	
1916	10	32.8	97.7	32.7	84.9	19.2	80.9	31.8	82.4
1917	11	46.2	103.7	12.3	78.6	37.6	83.8		

From these and other results (Jones, 1918) it is apparent that selfing in maize produces:

1. Strains which cannot be perpetuated.
2. Strains which can be perpetuated only with difficulty.
3. Strains which exhibit normal development but vary in amount of growth attained.

Whether selfed strains of maize can be obtained which yield as much as normal varieties is an unanswered question. Strains of timothy which have been selfed for 3 years at University Farm have yielded as well and are more uniform than commercial varieties. Similar results have been obtained by McRostie (1924), and Hamilton (1926) has recorded strains of sunflowers which have been selfed for 5 years and which are as vigorous or more so than commercial varieties.

EXPLANATION OF HYBRID VIGOR¹

The studies of the early hybridizers, Koelreuter, Gärtner, Knight, and others, gave results which can be summed up in a single sentence as follows (East and Hayes, 1912):

Crosses between varieties or between species often give hybrids with a greater vegetative vigor than is possessed by either parent.

Darwin made extended and careful studies of the effect of cross- and self-fertilization in plants. He conclusively proved that, in general, there is an advantage in cross-fertilization. While he noted some self-fertilized families he believed these would eventually perish. Lacking as he did a knowledge of Mendelian phenomena it was impossible for Darwin to develop as logical an explanation of these results as exists today. Darwin thought the results could best be explained by the nature of the sexual elements rather than in the act of crossing.

Several explanations of hybrid vigor have been advanced since the rediscovery of Mendel's law. In all cases heterozygosis has received a major place in the explanation. The results of these studies have been summed up as follows (East and Hayes, 1912):

1. The decrease in vigor due to inbreeding naturally cross-fertilized species and the increase in vigor due to crossing naturally self-fertilized species are manifestations of one phenomenon. This phenomenon is heterozygosis. Crossing produces heterozygosis in all characters by which the parent plants differ. Inbreeding tends to produce homozygosis automatically.

2. The phenomenon exists and is, in fact, widespread in the vegetable kingdom.

3. Inbreeding is not injurious in itself, but weak types kept in existence in a cross-fertilized species through heterozygosis may be isolated by its means. Weak types appear in self-fertilized species, but are eliminated because they must stand or fall by their own merits.

Biologists commonly believe that internal or external agencies do occasionally modify the germ plasm. It is also commonly accepted that somatic modifications do not impress themselves upon the germ plasm.

¹ A recent monograph by EAST and JONES (1919) presents in a clear and concise way the effects of inbreeding and cross-breeding in the light of modern theories of genetics. This publication has been used very freely in this section.

From the facts of segregation, as explained by the Mendelian law, and the acceptance of the theory of factor stability, what may be expected in self-pollinating a naturally cross-fertilized plant, such as corn, or what will result in later generations after making a cross in naturally self-fertilized plants, may be considered next.

Several slightly different formulæ have been advanced to show the theoretical expectation. The simplest formula for the percentage of homozygous types in any generation following a cross between different forms is $\left(\frac{2^n - 1}{2^n}\right)^m$. In this formula n is the number of segregating generations which has elapsed since the cross was made and m is the number of separately inherited allelomorphic pairs of factors involved. In self-fertilized organisms this would not absolutely hold unless all the progeny of each genotype were equally productive numerically.

If linkage is involved this modifies the numbers of homozygous individuals of the different classes but the percentage of homozygosis is the same as for independent Mendelian inheritance (Wright, 1921).

In artificially self-pollinating naturally cross-pollinated plants, such as corn, it is theoretically possible to select a completely heterozygous individual in each generation for self-fertilization and thus obtain no reduction in heterozygosis. Jones (1919) has worked out theoretical curves for 1, 5, 10, and 15 allelomorphic pairs of factors for from one to 10 generations of self-fertilization following a cross.

Some facts regarding the effects of self-fertilization in generations following a cross are apparent from a consideration of this figure. When only a single allelomorphic pair is concerned, the first generation of selfing reduces the percentage of heterozygous individuals by half. When a number of factor pairs are concerned reduction of the percentage of heterozygous individuals is comparatively slow for the first few years of selfing. At the end of 10 years the percentage of heterozygotes is very low whether the initial cross was heterozygous for 15 allelomorphic pairs or for a single allelomorphic pair. From the above discussion it is apparent that after several years of self-fertilization following a cross between different varieties a large percentage of the plants are homozygous and will breed true for their characters if self-fertilization is continued. The number of different biotypes which can be isolated from a cross depends upon the number of allelomorphic pairs of factors involved and their linkage relations.

Formerly, the heterozygous condition was believed to carry with it an increased developmental stimulus. It was also believed that this stimulus was greater when the mate to an allelomorphic pair was lacking than when both were present. The physiological cause of this growth stimulus was not known although it was recognized that "the greater the degree of heterozygosis the greater is the vigor of the resulting plant"

(East and Hayes, 1912). A considerable number of studies showed that the rapidity and amount of cell division was increased.

A Mendelian explanation of this growth stimulus, which is so frequently found in crosses, has been advanced. Jones (1918) has explained the vigor of F_1 which has been called heterosis on the basis of dominance and linkage. In comparing crosses with their parents, it is quite common to find that the F_1 generation has a higher value for nearly every growth character than has the average of the parents. Modern geneticists recognize that each character is due to the interaction of many inherited

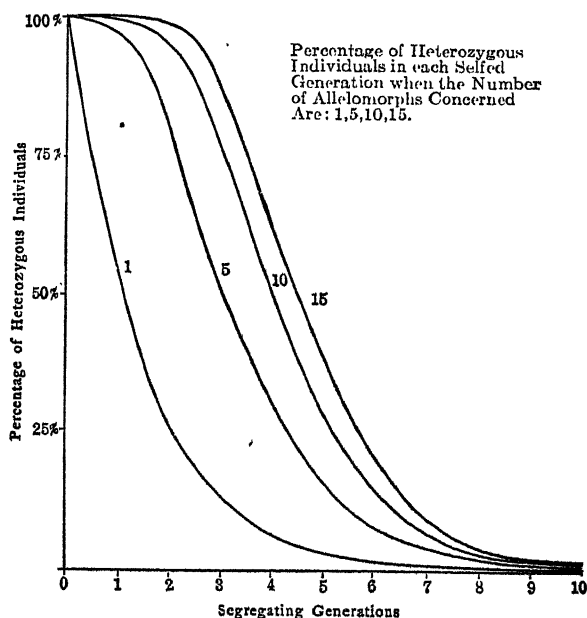


FIG. 16.—The percentage of heterozygous individuals and the percentage of heterozygous allelomorphic pairs in the whole population in each generation of self-fertilization. (After Jones.)

factors. If each growth factor gives as great an effect when heterozygous as when homozygous, or proves partially dominant when heterozygous, it would be easy to explain heterosis by the actual physiological growth development which is a part of the normal expression of particular inherited factors. Such an explanation was formerly advanced to account for heterosis but was considered unreliable, as it was difficult to account for the almost universal decrease in vigor when such plants as maize were selfed. This can be explained by the facts of linkage, as it is possible to have a greater number of different growth factors present in a heterozygous than in a homozygous individual. The explanation has much in its favor.

The difficulty of obtaining all desirable growth factors in one homozygous individual is that there are many undesirable genetic factors and these are linked in the same chromosome with desirable factors. The elimination of the undesirable leads naturally to the loss of some of the desirable.

A CLASSIFICATION OF METHODS OF BREEDING

It has been emphasized that there is a close relation between the normal mode of reproduction and pollination of a crop and methods of crop improvement. It is impossible, obviously, to breed self-sterile crops in the same manner as self-fertile ones. A monoecious plant like corn can be handled in a different manner than plants which produce perfect flowers. If vigorous selfed lines can be obtained in cross-pollinated plants, a somewhat different procedure may be followed than where selfing leads to great reductions in vigor. While special methods of breeding will be featured in relation to the discussion of individual crops, it appears desirable to outline methods in relation to the particular type of crop and problem concerned.

Breeding methods may be classified as follows:

1. Introductions

2. Selection.

- a. Mass selection:

- (1) In self-pollinated crops.
 - (2) In cross-pollinated crops.
 - (3) In dioecious crops.

- b. Individual plant selection.

- (1) In self-pollinated crops.
 - (2) In cross-pollinated crops (line breeding) without control of pollination
 - (3) In artificially self-pollinated lines.
 - (4) In dioecious plants.
 - (5) In clonally propagated lines.

3. Hybridization.

- a. Crosses in self-pollinated crops.

- b. Crosses of artificially self-pollinated lines.

- (1) Single crosses.
 - (2) Double crosses.
 - (3) Synthesized varieties.

- c. Varietal crosses.

Introductions.—New and improved crop plants are obtained by the cultivation of wild species, by the introduction of crops and varieties from foreign countries, and by the breeding of improved sorts. The present important crops grown in the United States were largely of foreign origin, although potatoes, cotton, corn, and tobacco originated in

the Western Hemisphere. Many of our crops were introduced by the early settlers, others are of more recent introduction. Examples of more recent introductions are soybeans and velvet beans from the Orient, the date palm from Africa and Mesopotamia, the fig from Asia Minor, and the navel orange from Brazil. The tepary bean, *Phaseolus acutifolius*, was raised many centuries ago in the arid Southwest by the Indians occupying these regions. It has been found to be a valuable plant for these regions. Sunflowers, native to this continent, are now being used for ensilage in regions where corn is not especially well adapted (Jones, 1925).

The Office of Foreign Seed and Plant Introduction, of the United States Department of Agriculture, conducts an organized search for new crop plants and for improved varieties in all regions of the world. Native wild species are also studied with the hope of obtaining new sources of material.

Because of the danger of introducing harmful fungous and insect pests, definite regulations for the introduction of plants and seeds have been made. Regulations are drawn up by members of the Federal Horticultural Board and Service and Regulatory announcements are published from time to time (see, for example, Marlatt and others, 1925). Quarantine regulations regarding the importation of stocks and seeds from foreign countries have been developed. Quarantine No. 37 is of most interest to the crop investigator. Under this law, field, vegetable, and flower seeds may be imported without restriction. Under Quarantine No. 39, however, restrictions regarding the importation of rice, wheat, oats, barley, and rye were made to guard against two dangerous plant diseases, *Urocystis tritici*, flag smut; and *Ophiobolus graminis*, take-all. Other quarantine regulations have been and will be drawn up from time to time for the purpose of protection against diseases and insect pests.

These quarantine regulations are of real value and should be adhered to scrupulously. Special permits may be granted for importation of seeds for breeding purposes when this is necessary.

New introductions of certain crops are studied by various officers of the Bureau of Plant Industry, United States Department of Agriculture. Thus the federal department takes the lead in trying out new crops and varieties although in some cases certain state experiment stations have conducted studies of great importance in this field.

Selections. *Mass Selection in Self-pollinated Crops.*—Mass selection is used by most breeders of self-fertilized crops as a means of keeping the variety pure. It consists either of selecting a large number of typical spikes, heads, or panicles; or, if the number of off-type plants is not very great they may be discarded by roguing. The latter procedure is an important step in the carrying on of a hand-selected seed plot. Mass

selection of self-fertilized crops is not so rapid or scientific a method as individual plant selection. Before modern principles of genetics were known and prior to the discovery of the pure-line hypothesis, mass selection was one of the usual methods used by the trained breeder.

Mass Selection in Cross-pollinated Crops.—Many improved varieties of cross-fertilized crops have resulted from mass selection although individual-plant selection and some system of controlling pollination are taking the place of the previous methods. Grimm alfalfa is a good example of the production of an improved variety by mass selection. Nature was the selection agent in this case (see Alfalfa). Many of the standard varieties of corn have been produced by farmers and mass-selection methods have been used rather largely. Familiar examples are Reid's Yellow Dent and Leaming. In fact, mass selection is the method which many trained breeders are recommending that the farmer use in keeping an adapted variety in a constant state of improvement. Dioecious plants may be bred in the same manner by mass selection as monoecious types and those which produce perfect flowers.

Individual-plant Selection in Self-pollinated Crops.—This method has been and will, without doubt, continue to be an important means of obtaining improved varieties of self-pollinated crops. It is the application of the pure-line hypothesis discovered by Johannsen. Several illustrations are given in a later chapter of improved varieties which were obtained by this method. It is essentially the first step after learning which are the better commercial varieties. It is the logical method to use if variations of the desired sort are already present in the variety. Nature produces the hereditary variations and the breeder isolates them by individual-plant or head selection. Natural crosses are one source of hereditary variations in self-fertilized crops although mutations do occasionally occur.

The individual-head or plant method consists of selecting several hundred heads or plants, propagating the progeny of each separately, making comparative-yield trials, and increasing the more promising variety or varieties for distribution.

Individual-plant Selection in Cross-pollinated Crops.—The progeny test or Vilmorin's isolation principle recognized that the only sure method of knowing the breeding value of a crop was the progeny test. With cross-pollinated crops, selections are made on the basis of the mother plant and selection practiced later in the more promising lines. Individual-plant progenies may be line-bred by isolating the strains a considerable distance apart largely to prevent crossing between them; or they may be allowed to out-cross with each other, as is commonly done in ear-to-row methods of breeding corn. By the use of these methods improved varieties of corn, rye, sugar beets, and other cross-pollinated crops have been obtained.

In Artificially Self-pollinated Lines.—Where it can be used advantageously, self-pollination is being tried out as a means of controlling the hereditary characters. By this method self-pollination is insured. Selection of desirable lines and plants within each line is made. After several years, lines which approach the homozygous condition are obtained. The many undesirable abnormalities present in some cross-pollinated plants can be eliminated and homozygous lines for disease resistance or for other characters may be isolated. Homozygous lines so obtained are of importance for fundamental physiological investigations and for the synthesis of improved varieties.

In some crops, such as timothy, sunflowers, and rye, vigorous selfed lines have been obtained. If such can be isolated, single lines may be used for the production of an improved variety. With corn it is difficult to obtain selfed lines which yield as well as normal varieties. The better selfed lines must be used, therefore, for the synthesis of improved varieties or for the production of F_1 crosses.

In Diacious Plants.—For this group both male and female plants may be selected and the hereditary characters of the parents determined by the progeny test of certain crosses. When the progeny of a particular cross breed true for the characters desired the new variety can be increased for distribution.

In Clonally Propagated Lines.—Individual plant, tuber, or bud selection in clonally propagated lines is for the purpose of separating a mixture of two or more clonal lines, the discard of diseased stock or the isolation of bud mutations. Mixtures occur frequently in clonal lines. As a rule, mass selection is used to discard diseased stock but individual selection is also practiced. The tuber-index method in potatoes consists in growing the progeny of a single eye, the discard of tubers which prove to be diseased by this test, and the increase of disease-free stock.

Extensive selections are being made in citrus crops and in sugar cane. It is a common belief among breeders of these crops that inherited changes occur frequently enough so that much progress can be made by selection in clonally propagated lines.

Hybridization. *Crosses in Self-fertilized Crops.*—This is the Mendelian mode of attack. Parents are selected on the basis of their characters and crosses are made between parent lines which in each case contain a certain desirable character or characters that the other lacks. Selection may be practiced until a considerable number of lines are apparently breeding true for the characters desired. Some few lines may be homozygous in F_2 for all characters. In the hybridization studies at Minnesota with small grains no attempt has been made in recent years to obtain homozygous lines until F_5 . Large populations are grown of each cross in F_2 and several hundred F_3 lines are grown. This gives a greater opportunity for selection than if small progenies are grown in F_2 and a small

number of lines in F_3 . After homozygous lines are obtained comparative-yield trials are made.

The segregating lines are planted so that individual plants can be studied. Each progeny, in each generation until homozygosis is reached, is obtained by planting seeds from an individual plant, head, or panicle. The comparable-yield trials are obtained from bulk sowings of lines which appear homozygous.

Crosses of Artificially Self-pollinated Lines.—A recent method of breeding in naturally cross-pollinated plants has been called "selection in self-fertilized lines." Self-pollination is induced by isolation of individual plants and lines are selected on the basis of their performance. Several methods are being tried with corn for the use of these lines. Three of them, discussed here, are called single crosses, double crosses, and synthesized varieties.

A single cross is the F_1 progeny of two lines. In a double cross four lines are used. A double cross consists of the F_1 progeny of two single crosses and has the advantage in corn that vigorous F_1 crosses are used as parents. Both single and double crosses are being tried in corn with the idea of growing F_1 hybrids as the commercial crop.

Synthesized varieties are the result of random matings in the progeny of several selfed lines which are recombined. The method has the advantage over single or double crosses in that seed can be saved by the grower and that yearly crosses need not be made. The extent to which F_1 crosses may be expected to be superior to synthesized varieties in yielding ability will depend on the relative yielding ability of pure lines and of F_1 crosses, and the number of different lines used in the recombination.

Varietal crosses are used extensively with horticultural crops which are frequently grown as clonal varieties. The genetic nature of the parents can be learned from the progeny of such crosses although, where possible, it may be desirable to determine the breeding value of a parent from the progeny of seed obtained by self-pollination. As a rule, varietal crosses are made for the purpose of obtaining certain desired combinations. They differ from pure-line crosses in that the parents are heterozygous and the F_1 plants are unlike each other. Hybrid vigor is obtained in varietal crosses as well as with pure-line crosses. There is the possibility with certain crops, such as corn, that synthesized varieties may be used as parents and F_1 varietal crosses grown as the commercial crop.

SUMMARY

The mode of pollination of a crop is important because the number and nature of the hereditary variations depends to a considerable extent on the frequency of cross- and self-pollination. In self-pollinated plants natural crosses occasionally occur and variation is induced. Self-

pollination after a cross leads rapidly, in later generations to homozygosis, and, as a rule, the progeny of individually selected heads, panicles, or plants of a variety breed true immediately. In the often cross-pollinated group natural crosses are more frequent. It is more difficult to keep the variety pure than in self-pollinated plants. Some method of isolation of individual plants and of varieties must be used but, in general, the same plan of breeding is desirable as with self-pollinated plants.

In both the self- and often cross-pollinated groups, the hybridization method of breeding is of great importance. Crosses are made between parents which are selected because each contains some important hereditary characters which the other lacks. Selection is practiced in the segregating generations and homozygous desirable types are compared under field conditions and the most promising, if sufficiently desirable, are distributed for commercial growing.

With the naturally cross-pollinated group of plants, two general methods of work are being used. In both cases selection is practiced. In one plan some method of controlled pollination is used, while in the other, selection is practiced but new variations constantly occur through natural crossing. Selection in self-pollinated lines is a means of isolating the more desirable strains. In some cross-pollinated crops, such as timothy, sunflowers, and rye, vigorous selfed lines may be obtained. In others, such as corn, it is difficult but not necessarily impossible to obtain selfed lines which are as vigorous or more so than normal varieties. Where F_1 crossed seed can be obtained relatively easily, as in corn, the growing for the commercial crop of F_1 crosses appears a logical procedure. The recombination of several lines with subsequent selection is a method which has certain advantages in the utilization of selected selfed lines. In certain cases single selfed strains may be sufficiently desirable so that they may be increased as new varieties.

CHAPTER VI

CONTROLLING POLLINATION

Methods of controlling pollination have received considerable attention. Protecting self-fertilized plants from occasional natural crosses would seem to be a necessity in careful studies of heredity. A knowledge of correct technic for crossing and selfing various crops allows the breeder to control the inheritance and in this way obtain the combination of characters which are desired. This entire field is one in which actual practice is needed before the worker can hope to accomplish best results. A few general principles will be given.

Selfing Plants Artificially.—Certain methods have already been worked out for particular crops. As an example, in the tobacco crop artificially self-fertilized seed may easily and cheaply be produced. The practical grower can well afford to save his seed by this practice. Before any of the blossoms have opened, the terminal inflorescence should be covered with a manila or hemp bag. The 12-pound size has been found satisfactory for this purpose. If a few flowers have already been pollinated these may be removed before bagging. After a week or 10 days has elapsed, the bag should be taken off and all flowers except from fifty to sixty removed and the dead corollas shaken off. After sufficient flowers have been fertilized the bag may be removed, as the seed will mature somewhat more rapidly than when enclosed.

Self-pollination of the tomato may be accomplished in very much the same manner as with tobacco. Small-sized bags are needed. In this case it is necessary to jar the flowering branches upon which the bags are placed, as the tomato does not set seed freely unless some such practice is followed.

Artificial self-pollination in corn is very easy. The ear and tassel may each be covered with a paper bag. The use of a transparent vegetable parchment bag to cover the ear shoot before any of the silks show allows the silks to be observed and facilitates pollination. As soon as the silks appear, a manila or hemp bag of the 12-pound size is placed on the tassel and pollination can be performed about 2 days later. If the silks are long, they may be cut off to a length of 2 to 3 inches which makes pollination somewhat easier.

Two men may well work together in pollination. One removes the ear bag and the other shakes the dead anthers from the tassel bag and pours the pollen over the silk. Care is needed in performing this opera-

tion to prevent cross- or uncontrolled pollination. In producing biotypes by self-fertilization the occasional cross may easily be rogued out as the crossed plant will plainly be seen the following year because of its vigor and other characters.

Hard showers or long-continued rains seriously interfere with the artificial pollination of corn, as the tassel bag becomes wet and makes the handling of the pollen difficult. A desirable method is to remove the tassel bags after each heavy rain and put on new ones. As a number of days elapse from the time the first pollen of the tassel matures until all is mature, the method of replacing tassel bags gives good results.

Jenkins (1923) has used a somewhat different method of pollination which has been found satisfactory in his studies. It has been called the "bottle method." The ear shoot is covered by a bag and as soon as a few silks emerge, the ear shoot is cut back $\frac{1}{2}$ to $1\frac{1}{2}$ inches and the bag replaced. After 24 to 48 hours a good brush of silks is ready to pollinate. The tassel required for pollination may be bagged at the time the ear shoot is cut back. It is thus protected for 1 to 2 days from foreign pollen.

Glassine bags $2\frac{1}{2}$ by 6 inches are used to cover the ear shoot before pollination. Heavy 12-pound tassel bags are placed over the silks preparatory to pollination. Small, wide-mouthed bottles were used and at the time of pollination they are filled with water and attached to the stalk just above the ear-bearing node. By placing the stem of the tassel in the bottle after placing the tassel in the bag and fastening the bag in place over the ear shoot, the technic of pollination is completed. Somewhat less satisfactory results were obtained at University Farm, St. Paul, Minn., with this method than by the ordinary one previously described, although very satisfactory results have been obtained by some workers.

Timothy and rye are handled quite satisfactorily by covering the spikes with the same parchment bag used for the ear shoot in corn pollination. The bags are 4 by $2\frac{1}{2}$ by $11\frac{1}{4}$ inches in size and waterproof glue is used. The bags are tied to stakes to prevent whipping in the wind. Nilsson (1922 and 1923) has worked out a satisfactory method for selfing sugar beets. After much experimentation with different methods of isolation, an effective and relatively easy method was worked out. On every plant about three isolations of single branches are made. In order to obtain more even ripening, the top of the branch is cut off and the lowest flowers that are already open are removed or at least marked as not selfed. A piece of cotton is wrapped around the base of the branch and a parchment bag (about 5 by 15 inches) is tied around the cotton piece. The upper end of the bag is held out by a little stick fastened to the corners. The stick as well as the lower end of the bag are tied to a bamboo stake.

A method used by Fergus (1922) has been found satisfactory as a means of self-pollinating red clover. One-pound Kraft paper bags were

used although vegetable parchment bags have been used more recently and have proved somewhat more satisfactory. The bag was placed over a head just as the petals were beginning to show and before any of the flowers had opened. Some of the leaves near the top of the stem were removed together with any small heads that were in the way. The bag was crumpled about the stem at the bottom and tied, allowance being made for the elongation of the stem after bagging. After 48 to 72 hours each bag was removed, the heads rolled gently between the thumb and fingers and the bags replaced. The hands were washed with alcohol after the selging of each plant.

Self-pollination of squash has been carried out at the Minnesota Station. A little practice helps in determining when a flower is about ready to open. The petals of both staminate and pistillate flowers are prevented from opening by placing a small rubber band around each one. On removing the band the following day the flower quickly opens if it is ready for pollination. The petals are then removed from the staminate flower and the anthers rubbed over the pistil. The artificially pollinated flower is protected from cross-pollination by placing a rubber band around the petals. After a few days the petals of the crossed flower abscise and at this time the stigma has turned brown and is no longer receptive. This method was worked out by John Bushnell. From a total of 600 pollinations made under field conditions in the summer of 1919, approximately 150 set fruit.

Technic of Crossing.—A thorough knowledge of flower structure of the species or variety to be worked with is essential before crossing is undertaken. It is important to know which flowers are the most vigorous and which set fruit the most freely. Many varieties of wheat, for example, produce several seeds per spikelet. The outer florets of the spikelets in the central part of the rachis are more vigorous and usually produce larger seed. In some *Solanaceae* (for example, the petunia) the later flowers form larger, healthier seed than those which first open (East, 1910c). After becoming familiar with the flower structure it is important to determine at what time of day the pollen is most easily collected and for what length of time the stigma is receptive. Environmental conditions modify the expression of these and other characters. However, some general rules for different groups of crops may be given.

Certain tools are essential for the work of pollination. For general work these are a small pair of thin, pointed scissors; a pair of forceps with thin, pointed blades which meet exactly and which are not too stiff; one or two dissecting needles; a hand lens; a pencil; and small string tags for recording purposes. Other special apparatus is necessary for difficult crosses.

Crossing of Small Grains.—The technic of small grain crossing is comparatively simple. Some practice, however, is necessary in order

to gain proficiency and to obtain a fair percentage of seeds set. In some of the earlier directions it was stated (Hays, 1901) that it was necessary to make crosses of wheat at about 4 o'clock in the morning.

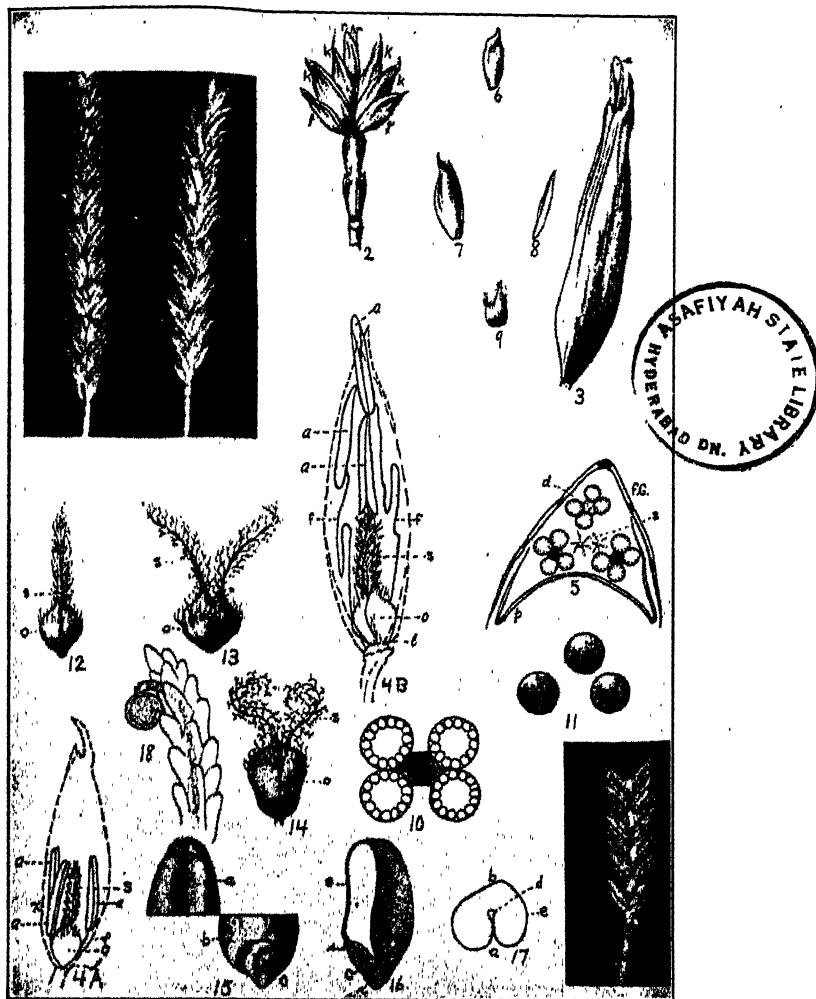


FIG. 17.—Details of wheat inflorescence.

Upper left, normal spikes; lower right, emasculated spike; 2, spikelet natural size; *f* and *g*, flowerless glumes; *k* and *r*, florets; 3, a single flower closed just after flowering, 3n; 4A, longitudinal diagram before flowering, $\times 2.5n$, *a* = anthers, *o* = ovary, *s* = stigma, *f* = filament; 4B = diagram after flowering; 5 = transverse floral diagram, 6n, *fg* = lemma, *p* = palea, *a* = anthers, *s* = stigma; 6, flowerless glume; 7, lemma; 8, palea, slightly reduced; 9, lodicule, 4n; 10, cross-section anther, 28n; 11, pollen grains; 12, ovary and stigma just prior to flowering; 13, at flowering; and 14, shortly after; 15, 16, 17, the mature seed. (After Bubeck and Clausen, 1918, after Hays and Boss.)

Leighty and Hutcheson (1919) have determined the period in which blooming takes place at University Farm, St. Paul, Minn., and at Arlington Farm, Rosslyn, Va. The spikes were examined at 7 a.m., 12 n., and 5 or 6 p.m. A flower was considered as having bloomed

when the glumes had opened appreciably. The period from 5 or 6 p m., to 7 or 8 a m. was referred to as night. Of 2,977 wheat flowers on 69 spikes, 1,492 bloomed at night and 1,485 bloomed during the day. About half of those which bloomed during the day bloomed before noon. These figures are given to correct the erroneous idea that it is always necessary to pollinate wheat early in the morning. Environmental conditions may be an important factor, for Salmon (1914), working in South Dakota, stated that blooming was practically completed before 7 o'clock in the morning.

Leighy and Hutcheson (1919) show that in wheat it is unsafe to leave the spikes uncovered after emasculation. Seeds were formed by 507 of 1,240 emasculated, unprotected flowers at University Farm, Minn. and 1,103 seeds were formed in 1,324 flowers similarly handled at Arlington Farm, Va. while less than 1 per cent of flowers emasculated and covered with paper bags set seed. Frear (1915), working with Turkey winter wheat, obtained 80 per cent seeds set on emasculated, uncovered spikes and less than 1 per cent on emasculated covered spikes.

Where greenhouse facilities are available, crosses may be made advantageously in the winter or early spring months. This method is used extensively by the Plant Breeding Department of Cornell University. When all conditions are favorable between 50 and 100 per cent of crossed seeds may be obtained.

Crosses, as a rule, may be made under field conditions and it is desirable to make several plantings so that plants of both parents may be in the same stage of maturity. The methods given here have been developed gradually and are those now in use at University Farm, St. Paul, Minn.

Wheat.—Emasculation is done while the anthers are green but beginning to turn yellow. A spike is trimmed to about eight or ten spikelets by removing the lower and upper spikelets. This leaves florets of about the same stage of development. The central florets are removed by pulling them out with the forceps. The anthers of the remaining florets are removed with a pair of forceps which are forced into the floret at the side by spreading the lemma and palea. A glassine bag 1.5 by 6 inches is placed on the emasculated spike and tied firmly with wrapping twine which had been previously cut in convenient lengths. A small marking tag is then used to label the plant. On one-half of the tag the name of the female parent is written and also the date of emasculation and the initials of the worker. Ordinarily, pollination is most successful if done two days after emasculation. This, however, will depend on the stage of development of the flower at the time of emasculation and on the condition of the weather. In exceptional cases the best seed setting has been obtained by pollinating 5 or 6 days after emasculation. Anthers of the pollen parent are gathered in the palm of the hand

and should be ready to dehisce. The glassine bag of the female parent is removed and a bursting anther placed on the stigma of each floret. The bag is then replaced and the pollen parent recorded on the tag with the date of pollination and the initials of the worker. The bags are left on the spikes until harvest as a protection from birds.

Oats.—The panicle is trimmed to about 15 to 20 spikelets and the secondary florets removed. A floret is held between the thumb and forefinger and the palet is pulled down and held with the thumb. The anthers are then removed and the palet is placed back in position. Pollination after 3 or 4 days has proved satisfactory. The glassine bags for oats are 3.5 by 8 inches. In other respects, oats is treated in the same manner as wheat.

Barley.—Emasculation of barley must be done before the spike has come out of the sheath. Lateral florets are preferably removed and the spike is trimmed to carry about 12 to 16 florets. Each floret is clipped off just above the tips of the anthers with a pair of scissors, and the anthers removed from above. This method was learned from Harlan of the United States Department of Agriculture. In pollinating, the dehiscing anther is dropped on the stigma from above. Bagging and labeling are the same as in the case of wheat. Pollinating 1 or 2 days after emasculation has proved satisfactory.

Rye.—The method is similar to that described for wheat with a few exceptions. About 16 spikelets may be left near the middle of the spike. The awns should be clipped off near the lemma for convenience. From 4 to 6 days may elapse between emasculation and pollination. As soon as the florets are found to be well open, the feathery stigma projects out considerably between the palet and the lemma. Good ripe pollen is collected in a glassine bag from the pollen parent. Each head to be pollinated is then stuck into the bag and dusted about, the stigmas becoming well covered with pollen.

Among the difficulties of artificial crossing in the field are unfavorable weather conditions. Too much rain or long-continued rains prevent work. Jellneck (1918) compared two methods of crossing wheats: (1) emasculation and pollination by placing a ripe anther in the floret; (2) emasculating spikes as usual and tying these with spikes of similar maturity belonging to the pollen parent and covering with a paper bag. In 1916 method 2 gave twice as great setting of seed as method 1. In 1917 conditions were very unfavorable and no seed was produced by method 1, while method 2 gave seeds in 24 out of 47 spikes. On these 24 spikes 50 per cent of florets produced seeds.

Rice.—Chao (1926)¹ has devised a method of crossing rice which he believes superior to any previous plan. He recommends that emascula-

¹ This description and literature regarding inheritance in rice was kindly furnished by L. F. Chao, a graduate student in genetics at the University of Wisconsin.

tion should be performed in the early morning before the sun rises or late in the afternoon. This precaution is taken because the pollen sacs may discharge the pollen grains when emasculation is done under bright sunlight. Flowers of some varieties mature immediately after emergence of the panicle from the leaf sheath while flowers of other varieties mature later. Rice flowers mature from the top of the panicle downward. From ten to fifteen spikelets are left on the top of the panicle. When the anthers reach about half the length of the lemma and palea (as can be seen by holding the spikelet against the bright sunlight), a short transverse cut is made near the tip of the spikelet with a pair of fine scissors and the anthers are removed through this cut with the aid of a fine pair of forceps. The panicle is rebagged and pollinated 15 to 24 hours later. Pollination is performed by inserting a mature anther into the cut surface of the spikelet and dusting the pollen cells over the stigma.

Crossing Large-flowered Legumes.—Oliver (1910) of the United States Department of Agriculture, has made excellent contributions to the technic of crossing. He emphasizes the fact that in a cross between self-fertilized varieties, only a few seeds are needed in F_1 . The large-flowered legumes, such as *Lathyrus*, *Phaseolus*, *Pisum*, *Stizolobium*, and *Vigna*, should be emasculated in the bud stage. The following account of crossing *Vigna*, the cowpea, is taken from Oliver:

In the evening it is found that the buds which will expand the next morning are quite large and easily manipulated in emasculating (*A*). Hold the bud between the thumb and forefinger with the keeled side uppermost (*B*); then run a needle along the ridge where the two edges of the standard unite. Bring down one side of the standard, securing it in position with the thumb; then do the same with one of the wings, which will leave the keel exposed. This must be slit on the exposed side about $\frac{1}{8}$ inch below the bend in the keel and continuing along until about $\frac{1}{16}$ inch from the stigma, which can be seen through the tissue of the keel. Bring down the section of the keel and secure it under the end of the thumb. This will expose the immature stamens, 10 in number. With a fine-pointed pair of forceps seize the filaments of the stamens and pull them out, counting them as they are removed to make certain that none are left (*C*). Allow the disturbed parts of keel, wings, and standard to assume their original positions as far as possible. Next detach a leaflet from the plant, fold it once, place it over the emasculated flower bud, and secure it in position with a pin or toothpick.

This prevents drying out. Flowers so treated and pollinated the next morning gave a large percentage of successful crosses.

Depollination with Water.—Oliver first used a garden hose in depollinating Grand Rapids lettuce. By cutting down the size of the opening with a smaller piece of rubber tubing a small jet of water was secured. After training this jet for a few seconds on flowers which had just opened, no pollen remained. Small pieces of blotting paper were used to remove excess moisture and then pollen was applied. Fifteen flowers of lettuce

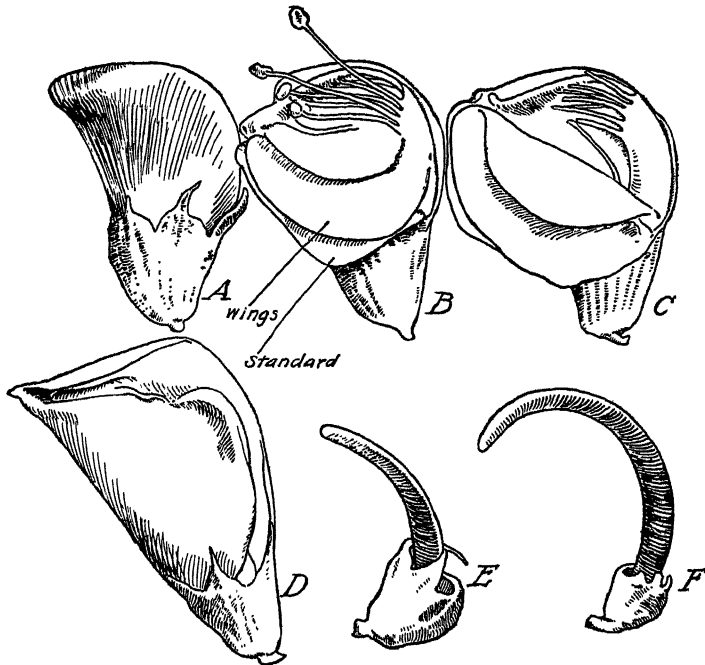


FIG. 18.—Flowers and young pods of the cowpea (twice natural size). (Copied from photograph by Oliver.)

A, flower bud showing condition on the evening of the day previous to opening of flower; B, flower in the bud stage showing how the floral envelope is opened to gain access to stamens for emasculation; C, flower with stamens removed showing the large stigma to the left; D, emasculated flower the next morning after pollination; E, the young pod the second morning after pollination; F, the same pod 48 hours after the pollination of the flower. (After Oliver.)

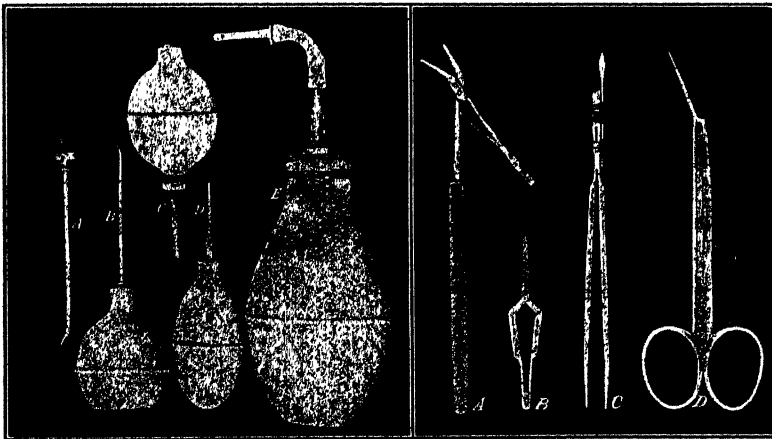


FIG. 19.—At right, A, scissors useful in removing small organs; B, self-closing forceps; C, forceps commonly used in emasculation with pin attached to the handle; D, scissors for severing large organs. At left, devices used in depollination of flowers; A and B, chip or water bulbs; C, water bulb with valve at bottom provided with celluloid ejector; D, old rubber bulb with glass tube inserted; E, "putty bulb" with attachment to give a small jet of water. (After Babcock and Clausen, 1918. After Oliver, 1910.)

were first crossed by this means and some seed was produced in each flower. The lettuce flowers and those of other closely related Compositae close soon after pollination.

Certain small rubber-bulb syringes have been found satisfactory for field work. These are used to depollinate the flowers with water. For a complete description of artificial cross-pollination of alfalfa flowers the reader is referred to Oliver. In the flower to be used as the female, the anthers have already dehisced but cannot perform the act of fertilization until the flower is tripped. To trip the flower and secure as small a percentage of pollination as possible is the aim. The technic of tripping and depollinating as well as the technic of crossing is a matter of practice. Oliver records that more than two-thirds of the alfalfa pollinations were successful by this method.

Use of Bees in Making Crosses.—Bees have been used frequently in making crosses. Williams (1925) has reviewed briefly some of these experiments and presented further data for red clover. The bees employed for making crosses were freed of viable pollen by washing them in tepid water in test tubes and drying them for a few hours before they were used. Cages of wire with six meshes to the linear inch and roofed over with glass proved satisfactory. When it was desired to cross plants which were some distance apart, cuttings were taken in the autumn and raised in pots. When the plants were in bloom the following year, the pots were sunk in the open and covered with small bee cages and the necessary bees were introduced. Honeybees could not be used to cross-pollinate red clover. The most efficient bumblebees for this purpose were *Bombus agrorum*, Fabr., *B. hortorum* Linn., and *B. helveranus* Seidl.

Crosses in Grasses.—Few artificial crosses have been made in grasses because of the obvious difficulties. Jenkin (1924) has succeeded in overcoming some of the difficulties, and has recorded successful crosses with *Dactylis glomerata*, *Phleum pratense*, and *Alopecurus pratensis*. The work was carried out in a large, cool greenhouse. The plants selected as parents were planted in pots in November and December of the preceding year. They were placed in the greenhouse when the first inflorescences were well emerged but not in flower and remained in the greenhouse until the hybridization work was completed. Separate inflorescences of the plants used as parents were bagged in order to obtain selfed seed and as far as possible no inflorescences of a species used for crossing were left unprotected in the greenhouse. The inflorescences used for pollen production were bagged. The pollen was collected and applied by means of a soft brush.

Emasculation was the most difficult phase of the work. It was found desirable to allow the inflorescences to approach within a few days of flowering before emasculation. Jenkins states:

For the emasculation of most grasses, relatively blunt-pointed forceps are used and without the aid of lens. Such forceps are less likely to pierce the anthers. For the emasculation of *Phleum pratense*, needle-pointed forceps with the aid of an $\times 8$ lens have been used.

The anthers are exerted under cool greenhouse conditions in the morning. Pollination has proved most satisfactory in the evening from 8 to 11 p.m., Greenwich time. Repeated pollination proved of value although no specific rules could be laid down. General rules given were as follows:

1. Pollinate for the first time as soon as the stigmas become exerted, or as soon after as pollen will allow.
2. Repeat pollination every day pollen is available in case none is available the next day.
3. Continue pollinating until the stigmas have all withered, or until pollen is no longer available.

Summary of Technic of Crossing.—Some important features of the technic of crossing may be summarized.

1. Make a careful study of the structure of the flower before commencing operations. This may be done with the aid of a dissecting microscope.
2. Determine which flowers produce the larger, healthier seeds and which set seeds the more freely.
3. Learn the normal method of blooming of the flower, the period of receptivity of the pistil, and the length of time the pollen grains are capable of functioning.
4. Procure the necessary tools and see that these are of an efficient kind for the work to be undertaken.
5. Be careful not to injure the flowering parts any more than is necessary. Do not remove the surrounding flower parts, *i.e.*, petals in flowering plants, glumes of grasses, etc. unless necessary.
6. A few crosses well made are of much greater value than many pollinations carelessly executed.

CHAPTER VII

SOME RESULTS OF SELECTION WITH SELF-FERTILIZED CROPS

In its broadest sense, selection is really at the basis of all animal or plant improvement by breeding. Evidence accumulated by early plant breeders indicated to them that selection of the most desirable plants for seed was highly profitable, irrespective of whether the plants were naturally cross or self-fertilized. Darwin believed that the mean type of any population could be changed by a plus or minus selection. It was left for Johannsen (1903) to point out the true significance of selection within a naturally self-fertilized crop.

Before discussing Johannsen's pure-line concept and its relation to the improvement of self-fertilized crops by selection, a brief survey of early work on improvement of naturally self-fertilized cereals is desirable.

EARLY INVESTIGATORS IN SELECTION OF SELF-FERTILIZED CEREALS

John Le Couteur and Patrick Shirreff were first to use the progeny test in making selections. The former did considerable work with wheat. In the early part of the nineteenth century he grew what he supposed to be a uniform variety. Professor La Gasca, of the University of Madrid, upon inspecting Le Couteur's wheat in the field, pointed out no less than 23 distinct forms. This observation led the latter to make a collection of 150 varieties. Le Couteur simply took it for granted that the progeny of any one individual would breed true. Patrick Shirreff, another breeder of cereals, who lived in the middle of the nineteenth century, worked along somewhat different lines. He searched for the exceptional plant to start a new variety, and discovered seven such varieties.

Frederic F. Hallett also followed rigid selection of individual plants in his wheat breeding. Furthermore, he proceeded on the theory that the selection of the best spike on the plant and the best seed on the spike would yield correspondingly the best plant. Le Couteur and Shirreff placed all the emphasis on the original plant selection, while Hallett believed he could improve the progeny of an individual plant by further selection. Needless to say, Hallett made no progress after the initial selection. A number of his improved varieties were introduced and widely grown.

Louis Leveque de Vilmorin formulated a breeding principle, as a result of a series of experiments performed by himself and his father, which was published in monograph form (1856). These early studies

were carried on with vegetables and the conclusion was reached that the only way to determine the breeding value of a plant was to grow and examine its progeny. Much study was made by the younger Vilmorin with the sugar beet. This is not a self-fertilized plant, but the principles learned have a direct bearing on selection with self-fertilized crops. In the first few years the problem of determining the sugar content of mother beets without injury to the roots received particular attention. Weighing a small ingot of silver in the juice extracted from a small piece of root was found to be an accurate method of determining density and thus sugar content. Roots of similar sugar content were then used as mother plants and their breeding nature determined. Some gave progeny with high sugar content without pronounced variability; other mother plants gave variable progeny some of which were high in sugar content and others much lower, while some mother beets produced progeny of such inferior sugar content that all were immediately discarded. Later, the sugar content was determined by means of polarized light (Babcock and Clausen, 1918). As an example of Vilmorin's results, may be mentioned a strain of beets which, after 3 years' selection, gave juice with an average density of 1.087 while unselected seed grown in the same field gave an average density of only 1.042. Andre Leveque de Vilmorin produced a desirable cultivated form of carrot by 3 years of selection from wild forms. Louis de Vilmorin also made a collection of wheats and other grains from all parts of the world. After 50 years of selection within isolated lines of wheat, no notable change was observed (A. L. and A. C. Hagedoorn, 1914).

Willet M. Hays, formerly of the Minnesota Experiment Station, was the first in America to adopt the "Vilmorin method" for small grains. In 1891 he introduced what is known as the centgener method of grain breeding (Hays and Boss, 1899). Briefly, it consisted of growing and harvesting a 100-plant plot from the progeny of each plant. Selection was continued the following year. The selections of most promise were increased and given extensive trials by farmers. By this method new forms of superior value were discovered.

The pure-line method of breeding self-fertilized crops was independently discovered and later adopted (1891) by the Svalöf Experiment Station in Sweden. The director of the station, H. Nilsson, was led to its adoption by the accidental discovery that only those plots planted with seed coming from a single plant exhibited uniformity (Newman, 1912). DeVries (1907) says:

To this accidental circumstance, combined with the exact scientific method of keeping extensive records, the discovery of the cause of the diversity of the cultures was due. For precisely those cultures which were derived from one ear only were found to be pure and uniform, all others offering to the eye a more or less motley assemblage of forms.

The fact that many of the agricultural varieties grown in Sweden at the present time are the result of this method of breeding is sufficient evidence of its success.

In addition to individual-plant selection, the older mass selection is sometimes used with self-fertilized crops. Mass selection is the selection of a group of individuals which seem to embody the desired characters. No attempt is made to grow the offspring of the different individuals separately and hence a pure-line study is impossible. In spite of this fact, mass selection sometimes has a place in correct breeding. For example, it may be advantageous to let nature eliminate non-hardy forms of a winter-wheat variety before beginning a study of individual-plant progenies.

SELECTION WITHIN A PURE LINE

Early in the twentieth century Johannsen (1903 and 1909) began his famous experiments with beans and barley which resulted in the discovery of facts which led to the development of the pure-line theory. Johannsen found that selection within a pure line was futile. Table XXXVII is typical of what he obtained by selection within each of 19 different pure lines of beans.

Since Johannsen announced his pure-line concept, several investigators working with other crops and other characters have verified his conclusions.

TABLE XXXVII.—SELECTION EFFECT DURING SIX GENERATIONS IN LINE I OF PRINCESS BEANS

Harvest years	Total number of beans	Mean weight of mother beans of the select strains		Difference, $B - A$	Mean weight of progeny seeds of select strains		Difference, $B - A$
		A-minus	B-plus		A-minus	B-plus	
1902	145	60	70	10	63.15 \pm 1.02	64.85 \pm 0.76	+1.70 \pm 1.27
1903	252	55	80	25	75.19 \pm 1.01	70.88 \pm 0.89	-4.31 \pm 1.35
1904	711	50	87	37	51.59 \pm 0.44	56.68 \pm 0.36	+5.09 \pm 0.57
1905	654	43	73	30	63.55 \pm 0.56	63.64 \pm 0.41	+0.09 \pm 0.69
1906	384	46	84	38	74.38 \pm 0.81	73.00 \pm 0.72	-1.38 \pm 1.08
1907	379	56	81	25	69.07 \pm 0.79	67.66 \pm 0.75	-1.41 \pm 1.09

Fruwirth (1917) made selections within a pure line of each of the following: lentil (*Lens esculenta*), vetch (*Vicia sativa*), snap bean (*Phaseolus vulgaris*), field pea (*Pisum arvense*), and white mustard (*Sinapis alba*), but failed to change significantly the mean of the character subjected to selection. In other words, the genotype was not altered. Fruwirth also conducted experiments within pure lines of oats. He selected for

number and length of hairs on the lower grain in addition to selecting for percentage of two-grained spikelets per plant. The work was carried on from 1906 to 1915 without effecting permanent alteration in the hereditary complex. The following table, taken from Fruwirth, illustrates a typical case:

TABLE XXXVIII.—SELECTION FOR PERCENTAGE OF BRISTLING IN OATS

Year	Minus selection			Plus selection		
	Per cent of bristling of			Per cent of bristling of		
	Parent	Progeny		Parent	Progeny	
		Mean	S. D.		Mean	S. D.
1907	^a	5.11 ± 0.68 ^b	1.68 ± 0.48 ^b			
1908	2.5	5.47 ± 1.37	4.32 ± 0.97	4.8	4.05 ± 0.88 ^b	2.78 ± 0.62
1909	0	4.70 ± 1.03	3.24 ± 0.72	9.2	4.75 ± 0.99	3.12 ± 0.69
1910	0.67	2.94 ± 2.36	11.80 ± 1.66	10.0	8.46 ± 1.61	8.06 ± 1.14
1911	0	0.14 ± 0.07	0.33 ± 0.05	21.9	8.88 ± 1.47	5.50 ± 1.04
1912	0	0.93 ± 0.22	0.85 ± 0.12	18.7	1.02 ± 0.35	1.65 ± 0.25
1913	0	1.20 ± 0.33	1.67 ± 0.24	5.1	3.58 ± 0.98	4.18 ± 0.69
1914	0	0.04 ± 0.09	0.44 ± 0.06	13.0	0.64 ± 0.25	1.25 ± 0.17
1915	0	2.65 ± 0.46	2.32 ± 0.33	5.7	3.14 ± 0.55	2.74 ± 0.39

^a Practically no bristles.

^b Mean error.

In the above table mean error is used instead of probable error (mean error × 0.6745 = probable error). The means, both in the minus and in the plus direction, show no effect of continuous selection.

In 1914 Hutcheson published the results of 13 years of continuous selection in wheat carried on at the Minnesota Station. Here again no significant effects of selection are found. In the following table a comparison of the yields for the first 5-year period with those of the last 5-year period is presented:

TABLE XXXIX.—COMPARISON OF AVERAGE YIELD PER PLANT IN GRAMS OF FIRST 5-YEAR PERIOD WITH THOSE OF LAST 5-YEAR PERIOD IN CONTINUOUS SELECTION OF WHEAT

Variety	First 5-year period	Last 5-year period
Hedgrow.....	2.67	2.34
Russian.....	1.99	2.18
Speltz.....	2.51	2.40
Kamouska.....	2.01	1.97
Polish 1.....	1.54	1.61
Polish 2.....	1.62	1.31
Average.....	2.06	1.97

In the tobacco-breeding work of the Connecticut Experiment Station (Hayes, 1913*b*) the inheritance of number of leaves was studied. The parental forms were grown with the hybrids for comparison. Although tobacco is naturally self-fertilized, the plants were bagged to insure self-fertilization. The behavior of the parental forms selected in a plus direction is shown. It is obvious from the data presented, that tobacco, like other self-fertilized crops, does not respond to selection within a pure line; at least not to a degree which would encourage the plant breeder to use this method of seeking improvement (see Table XL).

TABLE XL.—NUMBER OF LEAVES OF SUMATRA, 403; BROADLEAF, 401; HAVANA, 402; AND CUBAN, 405

Number	Year grown	Leaves of parent	Progeny			
			Range of variation	Total	Average	C V.
403	1910		24-31	150	28.2 ± 0.08	5.27 ± 0.21
403-1	1911	29	23-31	125	26.5 ± 0.11	6.64 ± 0.28
403-1-2	1912	29	21-32	151	26.2 ± 0.12	8.28 ± 0.32
401	1910		17-22	150	19.2 ± 0.05	5.00 ± 0.19
401-1	1911	20	16-22	108	19.1 ± 0.08	6.54 ± 0.30
401-1-1	1912	22	17-23	145	19.9 ± 0.07	6.03 ± 0.24
405	1910		16-25	150	19.9 ± 0.08	7.53 ± 0.28
405-1	1911	21	18-23	124	20.6 ± 0.07	5.29 ± 0.23
405-1-1	1912	23	17-25	150	20.9 ± 0.07	6.17 ± 0.24
402	1910		17-24	150	19.8 ± 0.07	6.98 ± 0.27
402-1	1911	20	16-25	143	20.3 ± 0.10	8.87 ± 0.35
402-1-1	1912	20	17-22	150	19.4 ± 0.05	4.59 ± 0.18

Love and Craig (1918*b*) reported on the effect of selection for height of plant within a pure line of oats. No evidence of selective effect was obtained, as is shown in the following table:

TABLE XLI.—SELECTION FOR HEIGHT WITHIN A PURE LINE OF OATS

Year	Average height of parents selected, in centimeters		Average height of offspring produced, in centimeters	
	Tall line	Short line	Tall line	Short line
1913	85.8	58.8	74.2	75.7
1914	86.9	60.4	82.6	82.9
1915	94.9	67.8	89.4	88.8
1916	97.1	74.9	95.9	94.5
Average.	91.2	65.5	85.5	85.5

An average difference of 25.7 centimeters in height of plant between the parent forms chosen, failed to change the genotype.

One of the old mooted questions among investigators of field crops was the relation between the weight of seed planted and the resultant yield. Earlier workers adhered to the belief that the selection of large seed would give increased yield. In a pure line of a self-fertilized crop, heavier seeds possess larger endosperms and consequently contain more stored food material for the young plantlet than the smaller seeds. It seems that it would be possible to have the environment during the germination period such that the larger seeds would have an advantage over the smaller ones. The important fact to bear in mind, however, is that all seeds of the same pure line have the same inheritance.

Some work has been done (Army and Garber, 1918) on the relation between size of seed planted and resultant yield in Marquis wheat. The seeds were individually spaced 4 inches apart. The relation between the weight of the seed in milligrams, and the resultant yield in decigrams was expressed by means of a correlation coefficient. The coefficients for the years 1914, 1915, 1916, and 1917 were 0.143 ± 0.038 , 0.088 ± 0.028 , 0.445 ± 0.020 , and 0.478 ± 0.024 , respectively. In this investigation each plant was given the same space for individual development. The results show that under these conditions relatively large amounts of stored plant food in the germinating seed may or may not give the resultant plants an advantage, depending on environmental influences other than the amount of endosperm.

Several investigators have attacked this problem from a practical viewpoint. Seeds were separated into light, medium, and heavy by means of a fanning mill. The productivity of the plants coming from the various classes of seed was compared under field conditions. Some investigators procured a slightly greater yield from plants produced by heavy seed than from those coming from light seed. Others obtained no such difference. Plants from medium or ungraded seed in almost all cases proved as productive as those from heavy seed. The work carried on at the Ohio Station may be taken as a typical example of these investigations.

TABLE XLII.—THE RELATION OF WEIGHT OF GRAIN TO YIELD IN WHEAT
7-year Average Results

Grade	Seed used, average weight per bushel, pound	Bushels per acre			Crop harvested average weight per bushel, pound
		Uniform seeding	Varied seeding	Average of both series	
First.....	61.6	31.3	31.3	31.3	59.4
Second.....	59.8	31.4	30.9	31.2	59.0
Third.....	57.7	31.3	30.7	31.0	59.0

Table XLII presents the average results (Williams and Welton, 1911) of an experiment with weight of seed wheat over a period of 7 years. The grades are first, second, and third, representing heavy, medium, and light seed, respectively. Two methods of seeding were practiced, namely, a uniform rate by weight and a varied seeding to obtain approximately an equal number of plants on equal areas.

In the case of oats (Williams and Welton, 1913) a greater difference was obtained between light and heavy seed, but the unscreened seed yielded only a little less than the large seed. The following table presents the average data of a 1-year period:

TABLE XLIII.--THE RELATION OF WEIGHT OF GRAIN TO YIELD IN OATS
4-years Average Results

Grade	Seed used		Bushels per acre			Crop harvested, average weight per bushel, pound
	Average weight per bushel, pound	Number per ounce	Uniform seeding	Varied seeding	Average of both series	
Light	27.5	1,052	59.0	59.0	59.0	28.6
Heavy	30.7	1,684	58.0	55.3	56.7	28.4
Unscreened	27.3	1,286	58.4	58.0	58.2	27.8

A current popular belief is that plants from large or heavy seeds yield more than plants from light or small seeds. The data collected by various investigators do not substantiate this view. As a matter of fact, from a practical viewpoint it would be difficult to demonstrate any increase in yield as the result of the use of a fanning mill. The fanning mill, however, is very useful in removing weed seeds or diseased light grains.

SELECTION FOR THE PURPOSE OF ISOLATING PURE LINES

The determination of the better selections requires at least 5 years. Accordingly, there have been consistent attempts to find some character or characters which were so closely associated with yield or other economic qualities that they were of actual selection value. If such could be found it would be possible to use them as checks on the yield results. Manifestly, they would be of especial value in the early period of head selection, for the results from short rows planted from individual heads are not very accurate indications by which to discard selections.

In this connection DeVries (1907) states that "correlation between botanical marks and breeding qualities are to be considered as reliable guides in the work of selection." As an illustration of such correlations, the belief that there is an association between three-grained spikelets of

oats and yield may be mentioned. Some of the early data collected at Svalöf indicated that such was the case. After 15 years of further study, five or six of the best yielding oat varieties were examined. Some were three-grained types and others were two-grained types. Newman (1912) in summarizing these results concludes that:

... there seems, therefore, to be no definite relationship between the yield of a given strain and the number of kernels per spikelet by which it is characterized.

The relationship between other characters was likewise studied, such as early maturity and high yield; short-haired rachilla and high brewing qualities in barley; weight of 1,000 grains in wheat, oats, and barley and yield; stooling with yield and quality; size of spike or panicle and yield. In some cases, there seemed to be a relation between yield or quality and some particular character, but when sufficient numbers were studied no consistent association between any one morphological character and yield was found.

Much investigational study has been made on this subject by others and similar conclusions have been reached. At the Minnesota Station correlations between yield and the following characters in wheat have been sought; stooling, height of plant, size of seed, date heading, and date of maturity. In some seasons the early varieties were the better yielders and in other seasons the later varieties.

Stooling was obtained from plots in which plants had room for individual development, and the correlation of stooling and yield was computed for 2 years for wheat, oats, and barley. Yield was obtained from the replicated rod-row test. The results showed no association between stooling and yielding ability.

Quite consistent association between weight of 1,000 plump seed and yield of wheat, as determined by the rod-row test was obtained and is given in the following table:

TABLE XLIV.—CORRELATIONS BETWEEN WEIGHT OF 1,000 PLUMP SEED OF *T. vulgare* AND YIELD

Number of selections or varieties in the population	Class and year	Correlation coefficient
70	Spring, 1914	0.431 \pm 0.066
70	Spring, 1915	0.519 \pm 0.059
35	Spring, 1917	0.580 \pm 0.076
63	Spring, 1918	0.109 \pm 0.084
54	Winter, 1916	0.356 \pm 0.080
83	Winter, 1917	0.436 \pm 0.060

Fairly consistent results of this nature would seem to show that weight of seed was associated with high yield in wheat. Montgomery (1912) isolated more than a thousand pure lines of Turkey winter wheat at the Nebraska Station and found both large- and small-seeded strains among the higher yielders. Similar results have been obtained at Svalof.

A study of the correlation between lodging and morphological characters of the stems of cereals has been carried out at the Minnesota Station (Garber and Olson, 1919). The number of fibrovascular bundles, the area of sclerenchyma cells in the cortex and bundle, and other characters were studied in relation to lodging. Stiffness and thickness of wall of the sclerenchyma seemed to be associated in oats but no such relation was found in wheat and barley. No other instance of a close association between any one of the characters studied and lodging was obtained.

There is considerable difference in beak length in bearded wheats (Clark and Martin, 1925). Kota, the spring wheat introduced by the North Dakota Station, and Kanred, which was produced by the Kansas Station, are both resistant to certain physiologic races of black stem rust, *Puccinia graminis tritici*. Both are bearded wheats and both have long beaks. As many ordinary spring wheats, such as Preston and most strains of Turkey winter wheat, have short beaks, the correlation between beak length and rust resistance is of value in helping to keep Kota and Kanred pure. In crossing experiments, however, it has been found that no close correlation exists between long beak and rust resistance.

Some correlations are of value in selection or in obtaining accurate data. Thus there is a direct correlation between size of head and yield of grain in sorghum or between size of ear and yield of grain in corn.

If one desires to classify a number of selections according to comparative maturity, reliable results may often be obtained by taking such notes as date of awn emergence in barley and date of heading in wheat and oats. In years favorable for normal development, a high correlation between date of heading and maturity has been obtained. In unfavorable years, date of heading is a more reliable indication of the inherited differences between strains in relation to their normal period of maturity than a note taken at maturity.

In general, it seems safe to conclude that no one character is closely enough associated with yield to be of selection value in picking out the highest yielding strain. It is possible, however, in many crops to weed out the very undesirable plants by inspection. The yield test must then be used to determine the better pure lines. This seems reasonable when it is realized that yield is the final result of many growth characters. A strain which excels in all characters, such as stooling, disease resistance, size of seed, size of head, fertility, etc., naturally will be a high yielder. As so many characters—of which the above are only a few of the more

easily seen—are essential to high yield, no single botanical character is of great selection value. This has led to the present method which is summarized as follows by Newman (1912):

Thus instead of basing the isolation of superior individuals purely upon botanical or morphological characters as was formerly the case, the principle has become to select a large number of individuals without special regard to such characters.

The value of these individuals is determined by the study of yield continued over several years.

Numerous experiments have proved the value of this method. In this connection it is of interest to point out progress that has already been made with self-fertilized crops.

Kanred winter wheat was discovered at the Kansas Experiment Station (Jardine, 1917) as a result of testing out 554 head selections made from Crimean (No. 1435 of the Office of Cereal Crops and Diseases, United States Department of Agriculture) and it is a rather striking example of what may be accomplished by this method of work. In a comparative trial conducted over 8 years, Kanred outyielded Turkey and Kharkov every year but one (Salmon, 1919). It is likewise the equal in milling and baking quality of other commercial varieties of Crimean. According to Parker (1924) it has added, already, an annual net value to the wheat crop of Kansas of over seven millions of dollars and has a potential value of over fourteen million dollars annually to Kansas farmers.

Red Rock winter wheat, which is highly satisfactory in Michigan, comes from a red seed picked out of a white wheat, Plymouth Rock, (Spragg and Clark, 1916). This is an example of selecting and increasing an individual obviously different from the type in which it occurred. The red seed may have been due to one of several causes, admixture, natural crossing, or a mutation. Whatever the cause, selection immediately isolated a wheat which was different in appearance and which proved valuable. On a percentage basis, the average yield of Plymouth Rock at the Michigan Experiment Station during the period 1912 to 1915 is 73.4. The yield of Red Rock for the same period is taken as 100.

Besides yield and quality other characters of economic importance may be improved by selection. The illustration on page 140, taken from Williams (1916), shows clearly what has been accomplished at the Ohio Station in the way of isolating a strain with stiff straw. The three pure lines shown are selections from the commercial variety Fultz.

Kisselbach and Ratcliff (1917) have reported in *Bulletin* 160 of the Nebraska Experiment Station the yields of numerous pure lines of Kherson together with the yield of the commercial variety for a 4-year period.

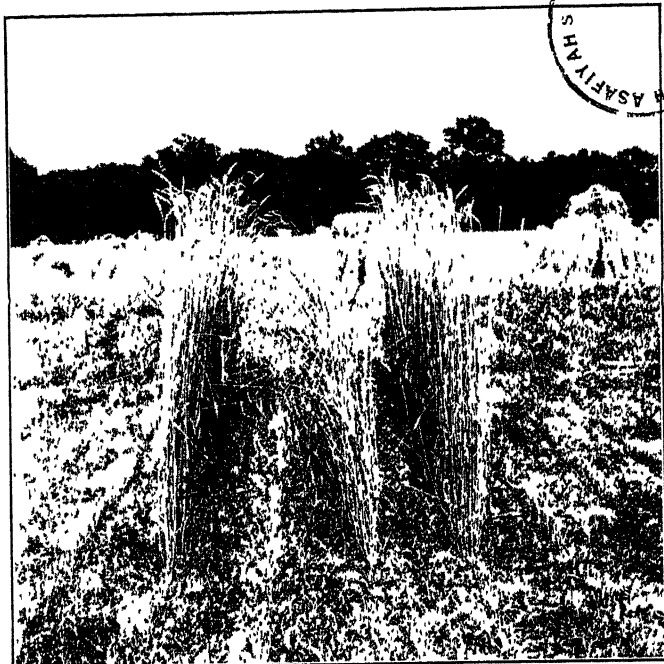


FIG. 20.—Variation in stiffness of straw in pure-line selections of Fultz wheat (After C. G. Williams.)

TABLE XLV.—YIELD TEST OF KHERSON OAT STRAINS GROWN IN FIELD PLATS, 1913 TO 1916

Strain number	Yield in bushels per acre				
	1913	1914	1915	1916	Average
Original	44 4	58.9	29 9	83.0	54.1
21	58 0	71 7	32.4	85.4	61 9
23	61.0	67 3	27.7	85 9	60.5
15	51 8	50 4	26 5	77 3	51.5
25	62 1	64 2	30 7	83 9	60 2
6	64 1	63 2	24 4	81.6	58.3
33	58 5	63.7	35 7	86.1	61.0
27	50 8	67.1	31 7	81.9	57 9
38	62 1	64 9	31 9	81.1	60 0
35	33 9	53 0	22.8	76.7	46.6
4	61.0	67 8	30 5	80 3	59.9
5	.	65 2	33 3	83 3	
19	.	50 1	21.4	74.8	

As shown by the last column of the table, only two of the 13 pure lines gave lower average yields than the commercial variety for the 4-year period. They are Nos. 15 and 35.

In a later report Kisselbach and Lyness (1924) give further data regarding these selections. Nebraska 21 is the most extensively grown of any of the pure lines and averages 2.8 bushels per acre more than Kherson from which it was isolated.

Other important varieties of oats have been obtained by selection. Cornellian was obtained from an individual plant selection and is a desirable variety in New York (see Love and Craig, 1924). Albion, Iowa 103; Richland, Iowa 105; and Iowar are valuable selections made and distributed by the Iowa station (Burnett and others, 1925), while Gopher, which is a stiff-strawed, white-seeded, early maturing variety, was obtained at Minnesota from a plant selection. Kansas introduced a variety of oats from Texas which proved to be a high yielder when compared with Red Texas oats. It was identified as Fulghum by Warburton in 1918. It has been compared with ordinary Fulghum and has proved much superior in yielding ability and also matures earlier. For this reason, the new variety was named Kanota to distinguish it from ordinary Fulghum (Salmon and Parker, 1921).

SELECTIONS IN OTHER SELF-FERTILIZED CROPS

An exhaustive account of the work that has been done in isolating and testing pure lines of self-fertilized crops would alone make a large volume. In this somewhat brief treatment only a few typical examples are chosen.

The Iron cowpea (Orton, 1911), which is resistant to wilt, is one of the notable examples of what has been accomplished by the introduction of a promising variety. The isolation of this form alone has produced thousands of dollars for the farmer. M. A. C. Robust bean (Spragg, 1919), which is a selection out of the ordinary navy bean, has proved to be very much superior in yield to the commercial variety. At the Svalöf Experiment Station (Newman, 1912), in Sweden, progress has been made in isolating pure lines of barley which possess superior brewing qualities.

These few examples show the value of selection as a means of crop improvement. The effect of selection is to isolate the more desirable types from the commercial variety. After this has been accomplished, crossing may be resorted to as a method of obtaining a variety which combines the desirable characters of several strains.

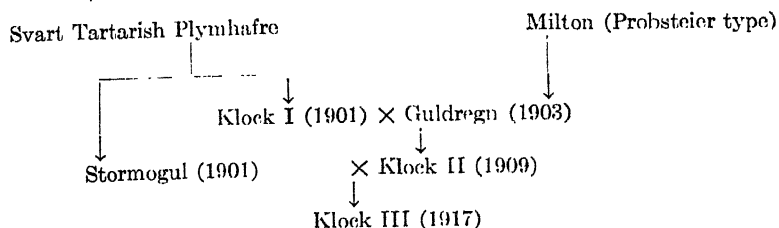
CHAPTER VIII

SOME RESULTS OF CROSSING AS A MEANS OF IMPROVING SELF-FERTILIZED CROPS

In the preceding chapters it was shown that the selection of a homozygous individual plant and the increase of its progeny isolated a pure line. No one of these pure lines contains, as a rule, all the characters desired. What usually happens is that one pure line excels in one character, while another is superior with regard to some other character. The only way in which the desirable characters belonging to different strains can be combined is by crossing and then selecting the desired segregate.

To attain success in this field, it is important to use as parents those forms which most nearly approach the combination of characters desired. The old idea of indiscriminate crossing in order to procure superior economic characters, such as yield, has been largely abandoned, which is reasonable from the knowledge of what selection accomplishes and of Mendel's law of inheritance in crosses. Love (1914) compared the yield of oat selections with hybrids which were the result of more or less indiscriminate crosses made by J. B. Norton. The average yield of the hybrids was but little higher than the average yield of the selections. It is probable that the comparison would have shown a greater difference if the parents had been chosen on the basis of their performance records. Two forms may be crossed because each possesses to the greatest degree the character sought, with the hope of obtaining transgressive segregation; or a cross may be made to combine different characters.

The Improvement of Black Oats at Svalöf.—Nilsson-Ehle (1917) has reported experiments carried on from 1901 to 1917 for the purpose of improving the black oats grown in Sweden. The native oats formerly grown had weak straw and lodged badly. Black Tartarian oats was introduced to overcome this difficulty. Little by little this form mixed with the native oats and probably naturally crossed to some extent. The resultant complex (Svart Tartarish Plymhafre) was especially suitable for selection and the isolation of desirable forms. This was done at the Svalöf Station. The selections, Klock 1 and Stormogul, maturing early and late, respectively, were obtained. Both possess stiff straw and Stormogul has good yielding ability. The improvement of the latter character was sought by crossing with higher-yielding, light-colored forms. The following diagram indicates the method followed. The varieties and strains were purified before the crosses were made.



Klock II is the result of crossing a good-yielding black oat of stiff straw (Klock I) with a high-yielding yellow oat (Guldregn). The new variety has the stiff straw of Klock I and the high-yielding ability of Guldregn. One selection from the cross of Klock II with Stormogul gave a strain, Klock III, which has the early maturity of Klock II, a somewhat higher-yielding ability than Stormogul, as well as non-lodging ability, which last character both parents possessed. In the following table the yields of three of the strains are shown:

TABLE XLVI.—RESULTS OF COMPARATIVE-YIELD TRIALS OF THE VARIETIES KLOCK II, STORMOGUL, AND A SEGREGATE KLOCK III OF A CROSS BETWEEN STORMOGUL X KLOCK II AS OBTAINED AT SVALÖF FROM 1912 TO 1916

Grain	Yield per hectare						Relative index Klock II = 100
	1912, kilo- grams	1913, kilo- grams	1914, kilo- grams	1915, kilo- grams	1916, kilo- grams	Average, kilo- grams	
Klock III.....	3,780	4,170	2,560	3,010	4,580	3,620	109.9
Stormogul.....	3,860	4,160	2,700	3,030	4,160	3,582	108.7
Klock II.....	3,730	3,870	2,360	2,280	4,230	3,284	100.0
<i>Straw</i>							
Klock III.....	5,060	4,530	2,470	3,825	7,850	4,747	100.3
Stormogul.....	5,810	5,330	2,850	4,550	7,630	5,234	110.6
Klock II.....	5,260	4,470	2,310	4,300	7,330	4,734	100.0

A Wheat Cross Made at Svalöf.—The highest yielding winter wheat grown at the Svalöf Station, reported by Newnan (1912), was a cross, Extra Squarehead II, No. 0290. This wheat is one of the offspring of Old Extra Squarehead X Grenadier II. It combines the winter-hardiness and rust resistance of the former with the stiff straw and high yield of the latter. As an average of 4 years' trial at Svalöf and Alnarp, this wheat has yielded 18 per cent more than Old Extra Squarehead and 8 per cent more than Grenadier II, which was next. No variety of winter wheat has proved so generally popular among the farmers of southern Sweden as Extra Squarehead II. It may be of interest to point out that, preceding the cross, hundreds of selections out of Grenadier II were examined in search of a pure line with the combination of rust resistance and high yield.

Wheat Breeding at University Farm, Cambridge, England.—Most of the wheat varieties grown in England are very susceptible to yellow rust (*Puccinia glumarum*). Biffen (1917) set himself the task of breeding a high-yielding, resistant form. He crossed American Club, which is very resistant to this parasite, with several susceptible varieties in order to study the mode of inheritance and develop a standard technic of operations. In all crosses the F_2 generations showed monohybrid segregation with resistance behaving as the recessive. The resistant individuals were rather clear cut, although they sometimes exhibited uredinia. The susceptible plants showed a wide range of variation. No recognizable morphological character has been found correlated with resistance.

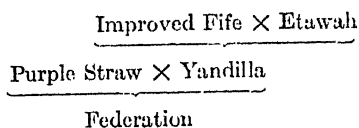
The constancy of resistance in wheats of hybrid origin has also been studied by Biffen. For the purpose he used a resistant strain produced from a cross between American Club, a resistant variety, and Michigan Bronze, which is one of the forms most susceptible to yellow rust. During 8 years of observation the hybrid variety proved just as resistant as the American Club.

A resistant variety of Russian origin, found among some Guika wheats, which was not adapted to local conditions, was crossed with Square Head's Master, the variety most commonly grown in England. Among the resistant offspring is one that gives considerable promise. Comparative trials of this wheat (Little Joss) over a period of 7 years show it to yield about 4 bushels per acre more than the best of the English and French wheats. The explanation for this would seem to be that Little Joss inherited the yielding capacity of Square Head's Master as well as the resistance of the Russian wheat parent.

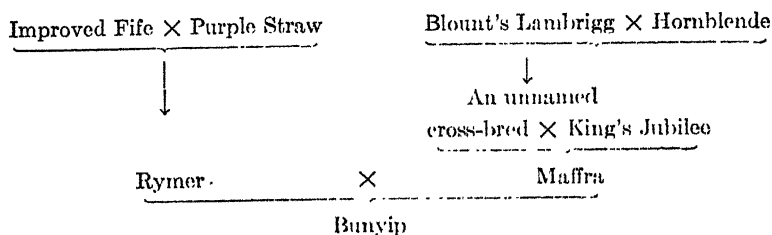
Farrer's Wheat Breeding in Australia.—Probably no one has made more wheat crosses that have proved valuable than William Farrer of Australia (Sutton, 1910). Most of his work was done without the application of a knowledge of the Mendelian principles. He, however, made crosses for definite purposes and in reality followed the Mendelian mode of work without recognizing the law involved. Farrer strongly featured composite crossing, *i.e.*, the crossing of parents which were themselves of hybrid origin. Federation, a variety very popular in southern Australia, was produced in this manner. As a typical example of Farrer's method, the history of Federation will be given somewhat in detail.

This variety was the outcome of a deliberate attempt to produce a wheat especially suited to gathering with a stripper, a harvester used in Australia. Federation is early maturing, stiff strawed, erect, and of somewhat short growth. Despite its rather unattractive appearance, it is one of the highest yielding wheats for the section in which it is grown. The upright habit makes it easy to harvest. Furthermore, the grains are held tight enough to prevent shattering but not tight enough to

interfere with the operation of the stripper. Federation resulted from a cross between the varieties Purple Straw and Yandilla. The parentage is indicated in the following diagrammatic scheme:



The history of the origin of Bunyip, another Farrer production, is indicated as follows:



Among other varieties produced by crossing which are of economic importance may be mentioned Comebacke, Cedar, Firbank, Bobs, Florence, and Cleveland.

Farrer's method of breeding seems to have been based on inducing maximum variation through composite crossing and then subjecting the progeny to selection. He was a keen observer and possessed ability to pick out forms which proved of economic value. This emphasizes the need of a knowledge of the characters of a crop with which the breeder is to work, which is as essential as a knowledge of laws of breeding.

Marquis Wheat.—If the spring wheat known as Marquis (Saunders, 1912) were the only one of economic importance which had been produced by artificial crossing, the practice would be justified. The early history of this wheat is somewhat obscure. It is one of the descendants of a cross between an early ripening wheat from India, Hard Red Calcutta ♀ and Red Fife ♂. The cross was made by A. P. Saunders, probably at the experimental farm at Agassiz, Canada, in 1892. The crossed seed or its progeny was transferred to the Ottawa Experimental Farm. Chas. E. Saunders who retired in 1923 took charge of the cereal breeding there in 1903 and immediately initiated a series of selections from the progeny of cross-bred wheats. The progeny from the cross made by A. P. Saunders was found to differ strikingly in gluten content of seeds. The laborious practice of chewing a small sample of each pure line was made the basis of selections. One of the high-gluten selections isolated from this mixture of types was named Marquis. It was first grown as a pure form in 1904

and the tests made in 1907 fully established its bread-making qualities. In addition to this character it is early ripening, thus often escaping rust, has stiff straw, high yielding ability, distinctive appearance of seed, and remarkably wide adaptations. These qualities have made it popular among the farmers in the spring-wheat belt.

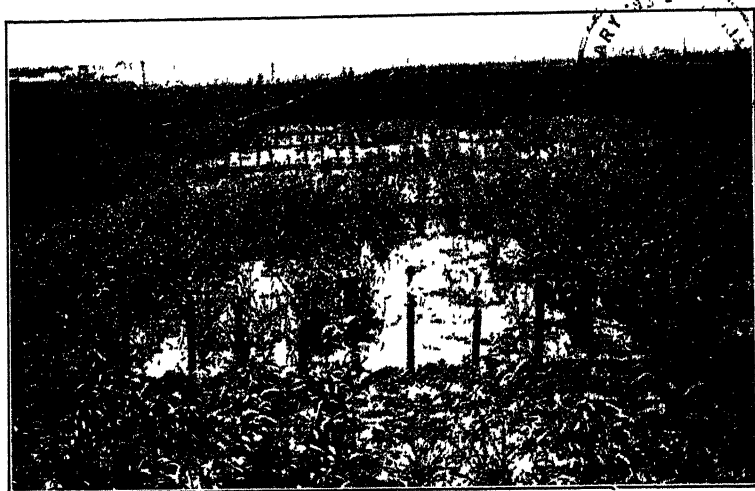


FIG. 21.—A section of the winter-wheat plant-breeding nursery in the spring of 1918. The three rows at the right are Minhardi, a very winter-hardy wheat produced from a cross of Odessa with Turkey. In right center are three rows of Turkey, Minn. 1487.

Winter-wheat Breeding at the Minnesota Agricultural Experiment Station.—One of the most urgent needs in order to bring about the successful production of winter wheat in Minnesota is a strain which will withstand the severe winters. This ideal has more or less been the goal of breeding operations from the first. Yield and quality also have been given considerable attention. Before attempting crossing, varieties were obtained from all over the world. Odessa, an awnless, red-chaffed variety of Russian origin, has proved most winter hardy, although some of the more recent Turkey selections are nearly as hardy. In the large number of crosses that have been studied since 1902 there is an outstanding fact worthy of emphasis. Of the different crosses made, none proved as winter hardy as the Odessa-Turkey combination, although numerous crosses between other winter wheats were studied. This shows the necessity of studying carefully prospective parental material to determine what should be used. When Odessa was used it furnished an hereditary complex capable of withstanding severe winters (Hayes and Garber, 1919).

Minturki (Minn. 1507) is a bearded wheat of the Turkey type obtained from this cross. It is as hardy as the Odessa parent, has high yielding

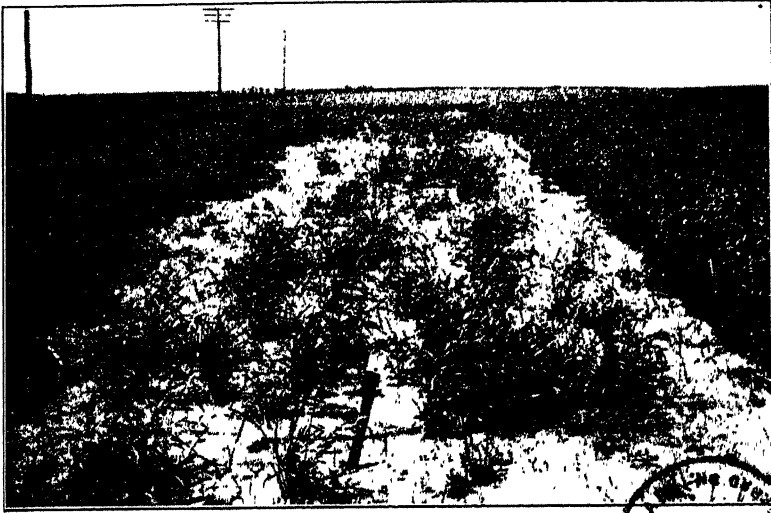


FIG. 22.—Turkey, Minn. 529. Grown in 1918. This variety winter-killed very badly.

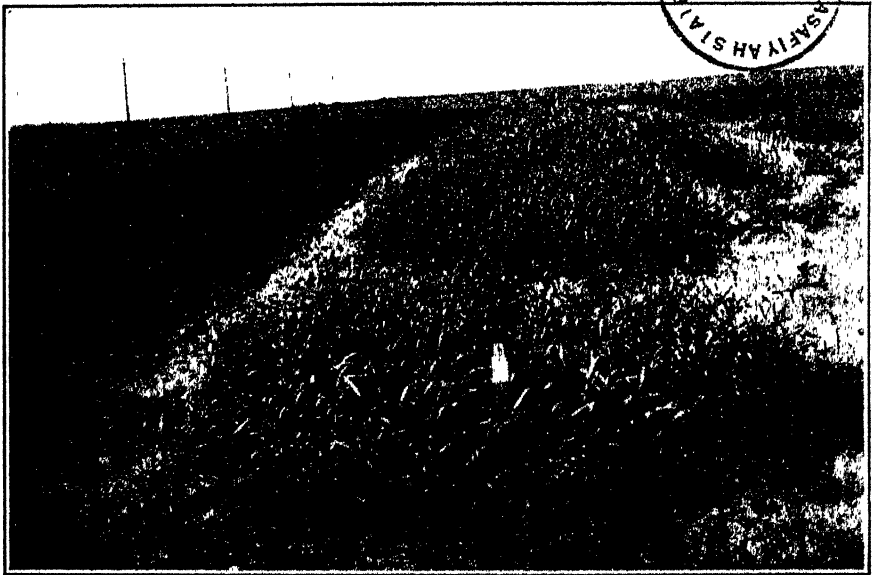


FIG. 23.—Minturki (Minn. 1507), a winter hardy variety of desirable agronomic type.

ability, and good milling quality for a winter wheat although not the equal of the better spring wheats in this particular. It has proved highly rust resistant under field conditions in southern Minnesota.

An awnless variety from this same cross, named Minhardi (Minn. 150b) has proved somewhat more winter hardy than Odessa and Minturki and is the equal in winter hardiness of any variety tested in North America but yields less on an average than Minturki.

At the present time, attempts are being made to improve quality by crosses of Minturki and Minhardi with the better spring wheats and with non-hardy winter wheats which appear somewhat superior to Minturki in milling and baking quality. This illustrates what is believed to be the correct procedure in plant breeding.

Breeding Wheat Resistant to Bunt (*Tilletia tritici*).—Gaines, at the Washington State Experiment Station, Pullman, began the work of breeding wheat for resistance to bunt by hybridization and selection in 1914. Since that time he has obtained considerable information on the comparative resistance of many varieties as well as the mode of inheritance of resistance in 26 different crosses (Gaines, 1925). One of the earlier crosses was made between Turkey and Florence. Turkey is a winter wheat of the Crimean group. It has a fair degree of bunt resistance as well as winter hardiness, drought resistance, and good milling quality. Florence is an Australian variety of spring wheat which, according to Sutton (1910), is a selection from a cross made in 1901. He says:

Florence is specially remarkable for its ability to resist the attacks of smut (bunt). In the severe tests to which it has been subjected the crops resulting from heavily smutted seed have proved to be almost entirely free from smut.

Each of the parent varieties Turkey and Florence is quite resistant although neither is entirely immune. Some of the hybrids of Turkey \times Florence proved immune while others were completely susceptible. Redit is one of the best selections from this cross. It is immune to bunt and has other desirable characteristics such as winter hardiness, high yielding ability, and good milling quality (Gaines, 1923, 1925).

Breeding Beans Resistant to *Colletotrichum Lindemuthianum*.—Extensive tests of the reaction between physiological strains of anthracnose and host plants were made at the Cornell Station. Four groups of beans were obtained: (1) resistant to both strains, (2) resistant to strain A and susceptible to strain F, (3) susceptible to A and resistant to F, (4) susceptible to both F and A. Wells' Red Kidney was practically immune to strain A and highly resistant to strain F, while Michigan Robust carried resistance to the F strain only. The latter is a white navy bean of superior yielding ability as was pointed out in the preceding chapter. McRostie (1919) crossed these two varieties to obtain a bean which possessed in addition to the characteristics of Robust, resistance to strain A of anthracnose. Segregation occurred for resistance to strain A on a simple Mendelian 3:1 ratio with susceptibility recessive. In the

second and third generations, a white navy bean homozygous for resistance to both physiological strains of anthracnose was obtained.

An Improved Strain of Tobacco.—Connecticut Havana tobacco introduced among Wisconsin farmers gave satisfactory results as to quality but the yield was low. Johnson (1919), of the Wisconsin Agricultural Experiment Station, attempted to overcome this objection by breeding. In 1909 a pure-line study revealed the fact that there were no



FIG. 24.—Tobacco No. 27. A pure-line strain with a high leaf number and a low breadth index of leaf. (After Johnson, 1919.)

less than three distinct morphological types present in the particular variety, grown at the experiment station, which was introduced from Connecticut. Selections Nos. 26 and 27 differed distinctly from the normal or prevailing type. Form 26 carried fewer leaves but of larger size than the normal, while form 27 possessed more leaves which were somewhat smaller in size than the normal. A cross between 26 ♀ and 27 ♂ was made in 1910 with the hope of combining the desirable features of the two forms. The success of the cross is indicated in the following data taken from Johnson:

TABLE XLVII—SUMMARIZED DATA OF MOST SIGNIFICANT CHARACTERS OF CONNECTICUT HAVANA No 38 TOGETHER WITH PARENT AND NORMAL STRAINS
Average of 8 years

Strain	Leaf number	Average of top, middle, and bottom leaves		Breadth index of leaf
		Length, inches	Width, inches	
No 26	14 2	20 0	11 3	56 5
No. 27	18 0	18 0	9 6	53 6
No 38 = 26 × 27	16 9	19 1	10 6	55 8
No. 33	15 5	18 2	9 8	53 8



FIG 25—Tobacco No. 26. A pure-line strain with a low leaf number and a high breadth index of leaf. Note the method of insuring self-fertilization by covering the terminal inflorescence with a manila paper bag. (After Johnson, 1919)

Number 33 is a desirable strain of the normal Connecticut-Havana type produced by continued selection and inbreeding. Breadth index is obtained by dividing the average leaf breadth by the average length and multiplying by 100. The table shows that by crossing, a form, No. 38, was obtained which combined somewhat the desirable features of

the parents (Nos. 26 and 27) and is superior in both number and size of leaves to the better pure line obtained by selection (No. 33). As an indication of the commercial value of the new form, it is estimated that 50 per cent of the total acreage (approximately 30,000 acres) in Wisconsin, is planted to this new variety.¹ Here is an example of crossing two closely related forms and of obtaining from the resultant progeny a strain of more commercial value than either parent.

The illustrations bring out more clearly some of the features of the parents and progeny.



FIG. 26.—Tobacco No. 38. This strain was produced by crossing No. 26, which excels in leaf breadth, with No. 27, which is homozygous for high leaf number. This new strain is more desirable than any other pure line form obtained. It is widely grown in Wisconsin. (After Johnson, 1919.)

Summary.—In this chapter concrete evidence of the value of crossing as a means of producing improved varieties of self-fertilized crops has been presented. Crosses should be made with a definite purpose in view and the parents should be selected on the basis of performance records. Just as a chemist requires a certain knowledge of the elements which he synthesizes into compounds, so also the plant breeder may make crosses much more intelligently if he is thoroughly acquainted with the prospective parental material. Promiscuous crossing as a means of producing improved forms is discouraged.

¹ Letter from JAMES JOHNSON (1926).

CHAPTER IX

METHODS OF BREEDING SMALL GRAINS

The progeny test is now recognized as the best means of determining the comparative productivity of varieties and strains. Vilmorin's isolation principle was first used in the United States in 1897 by Hopkins, of Illinois, for corn breeding, and in 1890 by Hays, of Minnesota, for small grains. Studies in field-plot technic and in crop genetics have led to standard methods of breeding self-fertilized crops.

One of the important steps for the breeder is to obtain a broad knowledge of the crop plant with which he is to work. This consists of a knowledge of the home of the plant, its wild and cultivated relatives, the existing varieties, and their important economic characters. It is also necessary to learn the needs of the crop for the locality in which the breeder is to work. The importance of this knowledge cannot be over-emphasized. After obtaining a fundamental knowledge of the crop, the work in crop improvement naturally falls under four heads: (1) introduction, (2) variety testing, (3) selection, and (4) crossing. Before taking these up, attention will be given to a system for recording plant pedigrees.

Methods of Keeping Continuous Records.—There are numerous methods of keeping records and as a rule each investigator will modify some general scheme to fit his own particular needs. It is also recognized that a plan which might prove satisfactory for an experiment station investigator who works only in one particular region might not be at all desirable for a federal worker who has charge of crop investigations over a wide area.

The Minnesota plan has proved quite satisfactory, although it is recognized that other methods of equal simplicity and value have been developed by other workers. It is given only as suggestive of the necessity of accurate records and as one means of attaining that end. When a new introduction is first brought to Minnesota it is given a Minnesota accession number and the history, source, and other data are entered in the number book for that crop. If the new introduction is a pedigreed form from a near-by state and seems promising, it is placed at once in the $\frac{1}{40}$ -acre plots and its value determined. In case it proves desirable it is recommended for Minnesota. Two such varieties are Marquis wheat and Victory oats. If the value of the new introduction is unknown, it is handled in the plant-breeding nursery.

Two types of rows are used in the plant-breeding nursery, plant rows and rod rows. Plant rows of various lengths are used depending upon the nature of the experiment. In plant rows the seeds are spaced $2\frac{1}{2}$ to 3 inches in the row and the rows are placed 1 foot apart. Plant rows are used when it is desirable to study individual plants. Rod rows are planted in bulk without individual spacing of seeds. They are not necessarily just a rod in length but are 1 foot apart as with plant rows.

New introductions from foreign countries are usually grown in plant rows the first year or two and their purity and characteristics determined. The very promising types, if homozygous, are tried in rod rows and may later be placed in $\frac{1}{40}$ -acre field plots. If apparently heterozygous or mixed, *i.e.*, if not a pedigreed variety, new introductions may be an important source from which to make plant or head selections.

The three groups, introductions, selections, and crosses, are given nursery class and stock numbers for means of identification. The year of the first test in Minnesota is also carried (except in the case of crosses where the year that the cross was made is used), together with a series number from 1 to as many forms as are handled in the class for the year and crop concerned. The following classes are used with the supposition that the forms were first tested in the nursery in 1920:

Class I-20-1, I-20-2, etc.....	Selections
Class II-20-1, II-20-2, etc.....	Crosses
Class III-20-1, III-20-2, etc.....	New Introductions

Supposing, for example, 20 new wheat introductions were grown, these would be classed as III-20-1 to III-20-20. All individual-plant selections are placed in class I if they are made from commercial varieties or new introductions. The year that they are first placed in the nursery is also carried, as well as the series number. These class and series numbers are not changed as long as the form is continued in the nursery trial.

Crosses are not given a series number until the strain gives evidence that it is homozygous. For the first few years the method of numbering used by the United States Department of Agriculture is followed. Thus a cross made between I-14-1 and I-14-20 is labeled at the time of crossing I-14-1 \times I-14-20. The female parent is written first. On growing this cross in F_1 a convenient number or letter is used. Later generations for the letter method would appear as A for F_1 , A-1 for F_2 , A-1-1 to A-1-200 if 200 plant selections were grown in F_3 . As soon as a cross is purified, that is, when particular selections appear homozygous, they are placed in the rod-row test and given a series number; thus the cross made in 1918 would be labeled as follows:

First year,	Class II-18, A
Second year,	II-18, A-1
Third year,	II-18, A-1-1 to A-1-200

If A-1-10 and A-1-50 appear homozygous and look promising, they may be placed in the rod-row test and receive series numbers as II-18-1 and II-18-2.

Books for bank figuring have been found to be satisfactory for the yearly field notes, a separate book being used for each crop

Planting lists show the order of planting in the field and are a record of the source of material. This allows a complete pedigree to be worked out for each crop. In the plant rows during the period in which homozygosity is being studied, it is necessary to have a record of the source in previous years. The following planting lists for a small part of spring-wheat studies illustrate plant-row histories in 1921 and 1922:

SPRING WHEAT, 1921 PLANT ROWS

Nursery stock No	Variety	1920 No	1921 No	Other notes
Check	Marquis		39	
Check	Kanred		40	
II-19F ₂	Kanred × Marquis	6-122	41	
II-19F ₂	Kanred × Marquis	6-123	42	

SPRING WHEAT, 1922 PLANT ROWS

Nursery stock No	Variety	1921 No	1922 No.	Other notes
II-19F ₃	Kanred × Marquis.	41-3	141	
II-19F ₃	Kanred × Marquis..	-4	142	
II-19F ₃	Kanred × Marquis. .	-5	143	

Thus the 1921 row 41 was planted from seed saved from a 1920 plant number 122 in row 6. Rows 141, 142, and 143 were planted in 1922 from seed of individual plants 3, 4, and 5 which were selected in row 41 in 1921.

With cross-fertilized crops, such as rye, nursery stock numbers are not used, and each planting-plan records the row numbers for the year in question and the previous source consisting of the row and the plant selected.

With self-fertilized small grains, the nursery stock number remains the same year after year. A planting plan for barley at University Farm in 1926 illustrates the method:

Name	Nursery stock number	1925 row	1926 rod rows			
			Series 1	Series 2	Series 3	Series 4
Manchuria.	Check	...	1-3	65-67	126-128	180-188
Velvet.....	11-20-10	260	4-6	68-70	129-131	189-191
Glabron.....	11-20-8	257	7-9	71-73	132-134	192-194

After obtaining yield and taking notes on grain characters, the yearly results are drawn off on 8½ by 11 paper, summarized, and filed for reference and further study. Only general notes are taken, such as date heading, date mature, height in inches, per cent lodged, degree lodged, per cent and kind of destructive diseases, botanical characters, grain color, plumpness and quality, weight per bushel, and yield.

New Introductions.—By means of new introductions the breeder is enabled to obtain varieties or strains which have been produced by other breeders, or native varieties from the original home of the crop. There is no value in attempting to produce a variety which is adapted to a particular condition if the qualities desired are to be found in some variety already grown in another locality or country.

The United States Department of Agriculture has a trained corps of workers who are constantly introducing new-plant sorts from foreign countries. At the present time the Office of Cereal Crops and Diseases of the Bureau of Plant Industry acts as a medium for the introduction of new varieties of small grains. Through cooperation with this office, promising new introductions are being tested in localities to which they seem adapted.

In small grains no conclusion can be drawn from the first-year test of a new introduction obtained from a widely different climate. Often the seed does not give a high percentage of germination or for some other reason the results secured are not even indicative of the value of the introduction. The first year the different introductions may well be grown in short rows. The following year a rod row of each new introduction may be grown as a part of the regular crop-breeding row trials, and yield and other characters determined. Those which are at all promising by this test may then be placed in the regular row trials and handled in the same manner as pure-line strains. After 2 or 3 years those introductions which give results of promise will be used as a basis for individual-plant selection, providing the introduction was not already a pure line.

Selection.—The plant-selection method is used for the purpose of isolating the best possible pedigreed strain of a commercial variety. If the variety is of considerable value a large number of individuals (500

to 1,000) may be selected. Often a smaller number is all that the breeder can afford to test. The number chosen will depend on the productive capacity of the commercial variety or new introduction which is used as the basis of selection. Plant selections are grown in short rows the first year, the same number of seeds being placed in each row.

Two general methods have been rather widely adopted for the initial head-selection plot. In either method the same number of seeds is placed in each row. The difference lies in the spacing of the seeds. Some prefer to place the seeds approximately the same distance apart in the row and at sufficient distance ($2\frac{1}{2}$ to 3 inches) that the plants can be separately observed. Others scatter the seeds in short rows, placing them so close together that individual plants cannot be differentiated at maturity. The latter method more nearly approximates the rod-row plan and needs less room. In either case the rows are usually 1 foot apart.

The field, after being carefully harrowed, is raked by hand, if necessary. It is then marked out by the use of a sled marker, from 7 to 12 rows being marked at a time. The rows are opened with a wheel hoe and covered either with it or a rake or a hand drag with numerous iron teeth. Some prefer a small nursery planter for seeding the rod rows.

Those selections which by field inspection seem to be of inferior vigor, to have weak straw or other undesirable characters, are eliminated before harvesting. A few others are discarded on the basis of yield, although the experimental error in a yield comparison of this kind is much too large to justify rejection. The following year each selection may be grown, if sufficient seed is available, in three systematically distributed 18-foot rows, 1 foot being removed from each end of every row before harvesting.

According to Love and Craig (1918a), J. B. Norton, of the United States Department of Agriculture, was the first to put the rod-row method into general use. By varying the length of the row and obtaining the yield in grams, it is possible to convert yields into bushels per acre by multiplying by a simple conversion factor. If the length of oat rows harvested is 15 feet and the yield is obtained in grams, the yield per acre in bushels may be obtained by multiplying by 0.2. For wheat and barley, if the rows harvested are 16 and 20 feet long, respectively, the conversion factor will be 0.1.

The rod rows are about twice as far apart as the rows made by a field grain drill. Some use one and one-half to two times as much seed per nursery row as under field planting, and hence the rate of seeding per acre does not differ materially in the two methods. Others use the same rate per row as in ordinary field seeding while at the Washington State Station 150 seeds per rod row were used. Still others correct rates of planting so that more seeds are used for larger seeded varieties. More data regarding these questions are needed. Rod row trials have been shown to

give results similar to those from field tests, although the average yield of the crop is not the same (Montgomery, 1913; Love and Craig, 1918a).

As has been previously noted, there are two general methods of work, *i.e.*, the use of single- and three-row plots. Three-row plots in which the central row only is used to secure yield are desirable as they help to control mixtures at planting and harvesting time, overcome competition between near-by varieties and help in obtaining more dependable data on lodging. They require more land and the cost is somewhat greater for planting and cultivating. In sections where soil heterogeneity is very great it is possible that the use of single-row plots and numerous replications may be somewhat better than three-row plots and fewer replications. On land that is well suited for field-plot work the use of three-row plots and three replications is advised.

After a strain has been grown for 3 years but may well be removed from the row-yield trial and either increased if it shows promise or discarded if it appears to be of no value. At Cornell new sorts are introduced to the farmers for trial directly from the rod rows. In many cases the new sort is finally tried in variety plots planted by the usual field-plot method. This gives an expression of yield under normal methods of planting and favorable field conditions.

Summary of Methods of Selection.—1. Determination of the varieties which possess economic possibilities. These may be commercial varieties or new introductions.

2. Head selection of these promising varieties.

3. Test of head selections in short rows. The very undesirable strains are eliminated in the field by inspection. A few may be discarded on the basis of yield or seed characters.

4. Yield determinations of the selections, using three plots of a single row each, systematically replicated, if seed is available.

5. Continuation of the row test. When land is well suited, it is believed that four systematically distributed plots of three rows each will give reliable results. Possibly the arrangement of selections of like nature together, the use of single rows and more replications, may be desirable under certain conditions.

6. Computation of a probable error for the method of test. The use of this probable error as a means of determining significant differences.

7. Increase of the better selections and either a trial by careful farmers or a further test in rod rows or field-variety plots followed by distribution of the better strains. If placed in field-variety plots, borders should be removed and each variety tested in replicated plots. Probable errors should be obtained and used as in the row trials.

From 5 to 8 years' time is needed before the new selection is introduced to the farmer.

Crossing.—The improvement of commercial varieties of self-fertilized small grains by the head or plant method of selection is a very easy process, although several years are required to do the work. The production of new forms by crossing is not so simple. A standard plan of attack has been developed which is the application of the Mendelian method.

The first step is the initial cross. Promiscuous crossing is not advised, but each cross should be the result of a determination of parents which most nearly approach the ideals in mind. By recombination of characters, there is the possibility of obtaining a sort which is more desirable.

The F_1 generation is grown so that each plant has space for individual development. A knowledge of the inheritance of characters allows those plants which are not crosses to be eliminated in F_1 . The F_2 generation plots should be as large as can be studied and each plant grown with enough free space that it may be examined. Numerous selections of plants which have desirable field and seed characters should be made. Each of these F_2 plants selected should be grown in an individual progeny plot in F_3 and individual plant notes taken. Selection of desirable plants should be continued in later generations. When plots show apparently uniform progeny of a desirable sort, the strain should be included in the rod-row tests and compared with standard varieties.

Knowledge of the results of continued self-fertilization in generations following a cross, shows the reliability of another method which was first used at Svalof, Sweden (Babcock and Clausen, 1918), and is now being tried by other investigators. It consists of growing a bulk plot of the cross for several generations. At the end of from 6 to 10 years, head selections may be made with the knowledge that a large part of these selections will breed true. The adoption of this plan will in a large measure do away with the technic of studying individual plants in a heterozygous population. It is desirable for those workers who would like to use crossing methods but who do not have time for individual-plant studies. It is not so rapid as the Mendelian method.

Technic of Harvesting, Thrashing, Etc.—Slight variations in methods are used by different workers. At Cornell rows of like kind are taken to the thrashing shed and hung head down until thrashed. At the Minnesota Station the straw is cut near the base, the bundles tied with the stake, labeled near the bottom, and the heads wrapped with a cheesecloth covering. Bundles of the same selection are then tied upright to a stake and later taken to the thrashing shed when needed. The row trials at the substations are harvested by cutting off the heads. These are then put into cloth sacks and shipped to the central station.

Several machines which can be cleaned easily have been devised for thrashing. The chief requisites of a machine to be used for experimental purposes are as follows: It should be easily cleanable and in so far as

possible there should be no ledges or ridges upon which seeds may lodge. The alternate thrashing of different nursery crops is a desirable procedure. Each of the plots of one strain of wheat may be thrashed separately in rotation and then a strain of oats may be thrashed in the same way. At the Minnesota Experiment Station winter wheat is thrashed alternately with barley, and spring wheat with oats. This plan helps materially to reduce the roguing of accidental mixtures from the plots.

Various machines have been made to assist in individual head and plant thrashing. A machine constructed by H. W. Teeter, of the Department of Plant Breeding at Cornell (Love and Craig, 1918*a*), is very satisfactory. As no screen or fan is used, all seeds are saved. After thrashing, the seed is passed through a wind blast. This machine is so arranged that mixtures may be avoided.

Technic of Breeding for Disease Resistance.—The importance of disease-resistant varieties of crops is recognized quite generally, for the success or failure of a crop often is dependent upon its manner of reaction to a particular pathogene. In most breeding problems it is essential to grow the experimental crop under normal conditions for the purpose of isolating the better sorts. In breeding for resistance to pathogenic diseases, the organism which causes the disease must receive as much attention as the crop itself and some method of creating an artificial epidemic of the disease must be evolved. Because of the nature of the problem, it appears that there is an opportunity for a cooperative attack on disease resistance with the geneticist and pathologist in the major rôles.

Certain information regarding the parasite which causes the disease in question is of primary importance to the breeder. Obviously, the constancy of the type of reaction between parasite and host plant is of major importance. Several years ago there was some doubt in the minds of many investigators as to the value of creating disease-resistant varieties. It frequently happened that a variety which appeared resistant one year was rather highly susceptible in a later trial. This was considered rather generally to be the result of a change in the virulence of the parasite and some explained the results on the basis of a change induced in the parasite by a different host plant. Thus Pole Evans (1911) speaks of a hybrid between resistant and susceptible strains of wheat which caused a change in the virulence of the parasite so that after living on the hybrid it was able to parasitize the resistant parent and to attack more vigorously the susceptible parent. Plant species which supposedly modified the virulence of the parasite were considered as bridging hosts. An explanation of these phenomena in agreement with modern genetic principles has been obtained. Extensive studies conducted primarily by pathologists have proved that many disease organisms are composed of numerous strains or physiologic races which are rather similar morphologically

but which differ widely in their parasitic capabilities. The development of this viewpoint has been gradual. It appears to be a natural viewpoint in the light of modern genetic principles. Numerous strains or physiologic races of many disease organisms have been found. There are some reasons for believing that the individual physiologic races are as constant as higher plants. In studying the genetic phases of disease resistance the individual physiologic races of the parasite must be used.

Methods of creating an artificial epidemic of the disease in question are various. For stem rust of oats where resistance is a dominant character and resistance and susceptibility are dependent upon a single factor pair, it is possible to grow 20 or 30 plants of numerous F_3 generations in the greenhouse and inoculate in the seedling state. The resistant lines can be determined by this means.

For stem rust of wheat the various hybrids are grown in a rust nursery. Cultures of all available physiologic forms of rust are grown on wheat plants in the greenhouse and these are transplanted to the field and serve as sources of infection. Spraying with suspensions of rust spores is resorted to also.

Spraying at about heading time with spore suspensions of *Helminthosporium sativum* and growing the barley cultures on the same soil year after year has proved satisfactory as a means of inducing an epidemic of the disease caused by this organism.

For smut of barley, wheat, and oats, smut spores may be mixed with the seed sown. At the Washington State Station a teaspoonful of smut is mixed with 75 to 100 seeds which are then placed in a small screen and the spores not attached to the seed are screened out.

In many disease-resistant studies, replication in the segregating generations has proved a valuable means of obtaining accurate knowledge of the breeding behavior. Thus two replicated F_3 rows were used in studies of resistance to *H. sativum* in barley for the F_3 progeny of each F_2 plant. Similarly, in studying resistance to *Puccinia graminis tritici* in wheat, two rows for each segregating line are grown and these are planted at different periods so that accurate data can be obtained. If a good rust note is obtained from both replicates the results are averaged. In some cases it is desirable to grow short rows of the hybrids in different localities in the segregating generations. Thus F_3 and F_4 generation hybrids, which are being bred for resistance to black stem rust, are grown at St. Paul, Waseca, Morris, and Crookston in Minnesota, at Brookings, S. D., and at Mandam, N. D.

CHAPTER X

CLASSIFICATION AND INHERITANCE IN WHEAT

Studies of genetics have led to the adoption of a particular meaning which is understood when an inherited character is spoken of. It is the final result of the interaction of many inherited factors plus the environment. The factors are the inheritance and the ultimate character is the manner of reaction under the special growing conditions to which the organism is subjected. What is inherited is the ability to react in a particular manner in a given place and not the character itself.

Genetic Classification.—Classification of cultivated varieties of crops is made in much the same manner as the botanical classification of wild species. With crops, there is as a rule considerable experimental evidence of genetic relationship. The ultimate aim of crop classification should be genetic in order that it may be of greatest value. Closeness of relationship as determined by the ease of crossing and the degree of sterility is frequently made the basis of species groups in some crops. In other crops no sterility is obtained in so-called species crosses. Only relatively stable characters which are not easily modified under different environmental conditions are considered of major classification value.

After placing cultivated crops in groups which are roughly analogous to botanical species, the next step is more clearly to separate different categories of a lower order of classification. These are the varieties. Varieties are not necessarily genetic entities but may be groups of similar forms which resemble each other more than individuals belonging to another variety. All members of a variety are similar to each other in major botanical characters.

Such a variety classification is of utmost importance. In the past the variety studies made in the United States by the different experiment stations or the federal Department of Agriculture have not always been comparable, as the same name has been used to refer to widely different varieties. More dependable results can be obtained only by the adoption of uniform variety names. Classifications of some crops have recently been made and in the next few years these will be improved further.

With self-fertilized crops, such as wheat, it is necessary to use pure-line varieties if the trials made at different stations are to be comparable. It is recognized by most plant breeders that pure lines of the same variety frequently differ widely in yielding ability although this fact has not

received the attention that it deserves by agronomists who are not primarily interested in crop improvement. Tests conducted by Stadler (1924) and Wiggans (1925) furnish evidence which show that a so-called variety is not an agronomic unit. Variety classifications are a necessary first step, however, in varietal standardization.

The central aim in crop-improvement work is to find or produce improved forms which when grown by farmers will excel in quality, productivity, or ease of handling. It is a decided advantage if the improved form can be distinguished from the varieties commonly grown in the locality by some botanical or morphological character difference. Kanred (Jardine, 1917) wheat is an example of a new variety with such a character. This variety, which was developed at the Kansas Station, belongs to the Crimean group of winter wheats. It gives larger yields on the average than Turkey or Kharkov selections and excels in resistance to some physiologic forms of black stem rust, *Puccinia graminis tritici*, and of leaf rust, *Puccinia tritici*. Its beak, i.e., the extension of the outer glume in the form of an awn point, is longer than in the common forms of Crimean winter wheat grown in Kansas. Marquis wheat, which is so widely grown as a spring wheat in the Northwest and Canada, differs in seed shape from other Fife wheats commonly grown in these sections. Forms belonging to the same variety may frequently exhibit differences in productivity and this may be the sole distinguishing character difference. Forms constantly differing from each other in one or more genetic factor differences which may be expressed as yield, quality, or disease resistance, or a minor botanical character and yet which belong to the same variety group, may be called strains. This is the lowest order of classification which can be adopted for seeded crops. With a self-fertilized crop the strain may also be a pure line in the original sense as used by Johannsen. With cross-fertilized crops the strain may be relatively pure from some particular character and may be heterozygous for other characters.

Inheritance studies of many of the present farm crops have been made. As crossing is the only means of inducing variation that can be carried out with success by the plant breeder, it becomes necessary to know how individual characters are inherited. It is true that yield is not a simple Mendelian character but is dependent on many inherited factors and their manner of reaction to the environment. At present, knowledge of inheritance may be used only as a guide in working with these characters. As a rule, the parental forms differ in botanical characters as well as in yielding ability. A knowledge of the mode of inheritance of each of these characters is essential to the rapid purification of a cross.

It is not desirable in a text on plant breeding to outline variety classifications in very great detail. As a rule the crops student will be familiar with such classifications before studying crop improvement. It seems

sufficient to indicate genetic relationship and to point out the characters which have been used.

Wheat Species Groups.—From the middle of the last century until the present time numerous crosses between wheat varieties and also between species groups have been made. Extensive crossing studies have led Tschernak (1914*a, b*) to conclude that the genetic relationships in wheat are as represented in the following table.

Several other species are described by Percival (1921) and Vavilov (1926) although the species given here are the ones of most importance.

TABLE XLVIII.—WHEAT SPECIES GROUPS

Group composition	Einkorn group	Emmer group	Spelt group
Stem species Spelt wheats	<i>T. aegilopoides</i>	<i>T. dicoccoides</i>	<i>T. spelta</i> wild form unknown
Cultivated forms Covered seed	<i>T. monococcum</i>	<i>T. dicoccum</i>	<i>T. spelta</i>
Cultivated forms Naked seed	Unknown	<i>T. turgidum</i> <i>T. polonicum</i> <i>T. durum</i>	<i>T. vulgare</i> <i>T. compactum</i>

Crosses reported by Tschernak between the einkorn and spelt groups so far have proved wholly sterile, while the einkorn emmer crosses have proved only slightly fertile. Similar results have been obtained by other investigators. The crosses between the covered emmer types and the naked and covered spelt forms or between covered and naked forms of the emmer group were partially fertile. Somewhat greater fertility was found in crosses between *T. polonicum* and the naked wheats of the spelt group, also between naked forms of the emmer group and the covered form of the spelt group. Some of the latter crosses seemed wholly fertile. Crosses between naked wheats proved wholly fertile.

Vilmorin (1880 and 1883) concluded that spelt and common wheats belong to one group and *durum* and *turgidum* to another, for crosses between any form in the first group with any form in the second group gave all cultivated forms of the spelt and emmer groups in later generations. Tschernak (1913) obtained similar results only from crossing solid- and hollow-stemmed varieties of the respective groups and only obtained *polonicum* forms when using *polonicum* as one of the parents.

T. dicoccoides was reported as being found wild as early as 1885. Aaronsohn (1910) found many wild forms of *T. dicoccoides* in Palestine. Love and Craig (1919*b*) have produced *T. dicoccoides* synthetically by

crossing durum and common varieties, which indicates rather close genetic relationships between these forms. Aamodt and Levine (1925) compared the reaction to black stem rust of the synthetic wild form obtained by Love and of *T. dicoccoides*. Both types gave similar reaction to several physiologic forms. It is essential to point out that all crosses between the cultivated naked emmer wheats with naked wheats belonging to the spelt group are not entirely fertile. Indications of



FIG. 27.—Wild wheat from Palestine and the New Hybrid. Here is shown a spikelet of the true wild wheat and one of the hybrid forms. (After Love and Craig, 1919.)

partial sterility are generally apparent if the results are carefully analyzed (Kezer and Boyack, 1918, Freeman, 1919; Hayes and others, 1920).

Sax (1921b) has studied sterility in F_1 species crosses using six species. These were *T. monococcum*, *T. durum*, *T. turgidum*, *T. polonicum*, *T. vulgare* and *T. compactum*. He based his results on the sterility of the F_1 as determined by the number of seeds set per spikelet and the percentage of sterile pollen grains. The results are presented in the following table:

TABLE XLIX.—STERILITY IN F_1 SPECIES CROSSES IN WHEAT

	Group number	Grains per spikelet		Per cent poor pollen	
		Number of tests	Average number of grains	Number tests	Per cent poor pollen
<i>T. monococcum</i>	1	1	0.97	1	0.3
<i>T. durum</i>	2	1	2.91	1	1.9
<i>T. turgidum</i>	2	1	1.93	1	1.5
<i>T. polonicum</i>	2	1	1.85	1	1.6
<i>T. vulgare</i>	3	4	2.33	3	1.1
<i>Turgidum</i> × <i>monococcum</i>	2 × 1	1	0.00	1	97.7
<i>Vulgare</i> × <i>turgidum</i>	3 × 2	3	1.39	1	15.2
<i>Vulgare</i> × <i>durum</i>	3 × 2	6	0.72	5	15.7
<i>Vulgare</i> × <i>polonicum</i>	3 × 2	2	1.13	2	15.5
<i>Vulgare</i> × <i>vulgare</i>	3 × 3	5	2.93	1	0.4
<i>Durum</i> × <i>turgidum</i>	2 × 2	2	3.60	1	0.9
<i>Durum</i> × <i>polonicum</i>	2 × 2	1	2.61	1	1.2

With the results of this experiment as a basis, Sax obtained the same grouping as Tschermak although the sterility results were similar to those obtained at Minnesota.

1. Einkorn group: *T. monococcum*. All varieties cross fertile; sterile or only slightly fertile with emmer and spelt group.

2. Emmer group: *T. dicoccum*, *T. durum*, *T. turgidum*, and *T. polonicum*. All species and varieties cross fertile; partially sterile with spelt group; sterile or slightly fertile with einkorn group.

3. Spelt group: *T. spelta*, *T. vulgare*, and *T. compactum*. All species and varieties cross fertile; sterile with einkorn group; partially sterile with emmer group.

Blaringhem (1914) crossed einkorn with *T. durum* and *T. turgidum* and obtained F_1 plants. Some seeds set on the F_1 and in the later generations some plants were fertile. Tschermak believed these seeds on F_1 plants were the result of natural crossing.

Wheat species have been classified by Vavilov (1914) according to susceptibility to *Puccinia triticina*. The groups were similar to those obtained as a result of sterility studies. They are as follows:

IMMUNE	RESISTANT	SUSCEPTIBLE
<i>T. monococcum</i>	<i>T. durum</i>	<i>T. vulgare</i> (a few immune)
	<i>T. polonicum</i>	<i>T. compactum</i>
	<i>T. turgidum</i>	<i>T. spelta</i>

T. dicoccum produced both resistant and susceptible varieties.

Zade (1914) determined three groups of wheat species as a result of serological relationships. Results were determined by using a serum of the different wheats and determining the reaction with the antigen of the wheats of the same group and those of the different groups. The following method of procedure was used.

The extract of the different cereal species was prepared by grinding a quantity of seeds in a mill. For 10 grams of the meal, 75 cubic centimeters of a physiological salt solution was used (0.85 gram NaCl to 100 cubic centimeters H_2O). A part of the extract was reserved and another part injected into a rabbit. Blood from the injected rabbit was then carefully filtered and to this blood serum various concentrations of the original solution were added. Three readings were taken:

1. The number of minutes before a slight precipitation was observed.
2. The number of minutes until medium precipitation.
3. The number of minutes which elapsed before heavy precipitation was observed.

In the following table only a concentration of 1:10 of the extract of the cereal meal on a physiological salt solution is recorded.

Strength of physiological salt solution of 1:10	Precipitated solution							
	<i>T. mon.</i>	<i>T. dicoc.</i>	<i>T. dur.</i>	<i>T. turg.</i>	<i>T. pol.</i>	<i>T. spelta.</i>	<i>T. vulg.</i>	<i>T. comp.</i>
<i>T. monococcum</i>	1	3	4	3	3-4	4	3	3
<i>T. dicoccum</i>	3-4	1	2	2	2	3	3-4	3
<i>T. durum</i>	5	2	1	2	2	3	3-4	3
<i>T. turgidum</i>	7-8	3	3	2	3	5	4-5	5
<i>T. polonicum</i>	6-7	3	3	3	1	5	4-5	5
<i>T. spelta</i>	3-4	3	3	3	3	1	2	2
<i>T. vulgare</i>	5-6	3-4	3-4	4	4	2	1-2	2
<i>T. compactum</i>	5-6	4-5	4-5	5	4-5	3-4	3	2

The results of this experiment likewise place wheat species in three main groups.

The wheat groups were found to be separated in a similar way on the basis of pollen size (Sax, 1921b).

Name	Group	Diameter of pollen grains in microns	Average
Einkorn	Einkorn	51.5	51.5
Kubanka (<i>durum</i>)	Emmer	55.5	56.3
Alaska (<i>turgidum</i>)	Emmer	57.1	
Hybrid 143 (<i>vulgare</i>)	Spelt	60.1	60.2
Marquis (<i>vulgare</i>)	Spelt	60.3	

The wheat species may be classified also on the basis of chromosome numbers. Various early workers (Overton, 1893; Körnicke, 1896; Nakao, 1911) reported eight as the haploid number in *T. vulgare*. In 1918 Sakamura reported the following chromosome numbers for each of the important species.

<i>T. vulgare</i>	42 diploid	} Vulgare group
<i>T. compactum</i>	42 diploid	
<i>T. Spelta</i>	42 diploid	
<i>T. turgidum</i>	28 diploid	} Emmer group
<i>T. durum</i>	28 diploid	
<i>T. polonicum</i>	28 diploid	
<i>T. dicoccum</i>	28 diploid	} Einkorn group
<i>T. monococcum</i>	14 diploid	

These counts have been verified by Sax (1921*a*), Kihara (1919, 1921, and 1924) and Watkins (1924). Kihara (1924) found that the species of *Aegilops* contained 28 chromosomes, while Percival (1926) found three groups of species of *aegilops* with 7, 14, and 21 chromosomes haploid, respectively.

Chromosome Behavior in Wheat Species Hybrids.—Type examples of chromosome behavior in crosses between related species which differed in chromosome numbers were given in the chapter entitled Plant Genetics. Fairly extensive studies have been made of chromosome behavior in wheat species crosses and between crosses of *Triticum* species with *Aegilops cylindrica* and with cultivated rye. Some of the more interesting results will be summarized. In crosses between winter rye, which contains 7 pairs of chromosomes, and *Triticum vulgare* which were studied by Kihara (1924), the somatic number of F_1 was 28 as would be expected. In diakinesis there was only a very loose affinity between the chromosomes of wheat and of rye and 7 complete bivalents were not found although in one case 3 bivalent chromosomes were observed. All of the univalents do not divide equationally in the heterotypic division and division both at the heterotypic and homotypic stages is very irregular. In contrast with this, fairly uniform results were obtained in both the heterotypic and homotypic stages of the F_1 generation of crosses between *T. dicoccum* and *T. vulgare*. The F_1 plants contained 35 chromosomes. The 14 chromosomes of dicoccum paired with 14 of vulgare making 14 bivalents and there remained 7 univalents. In the heterotypic division the bivalents separated and 14 chromosomes passed to either pole. The seven univalents split longitudinally and passed to either pole, thus producing daughter cells containing 21 chromosomes. At the homotypic division the 14 univalents which formerly were members of the 14 bivalent group divided longitudinally and passed to either pole. The remaining 7 univalents which already had performed their equational division passed at random to either pole. The daughter cells contain 14 to 21 chromo-

somes and the frequencies with which each of the numbers will be produced are given by the expanded binomial $(1 + 1)^7$.

Gaines and Aase (1926) have summarized chromosome relationships in wheat species crosses in a very interesting manner. The summary given here is quoted directly from their paper:

It seems significant in this connection that when *Triticum monococcum* L. (var. *Hornemanni* Keke.) with 7 chromosomes is crossed with *T. turgidum* L.

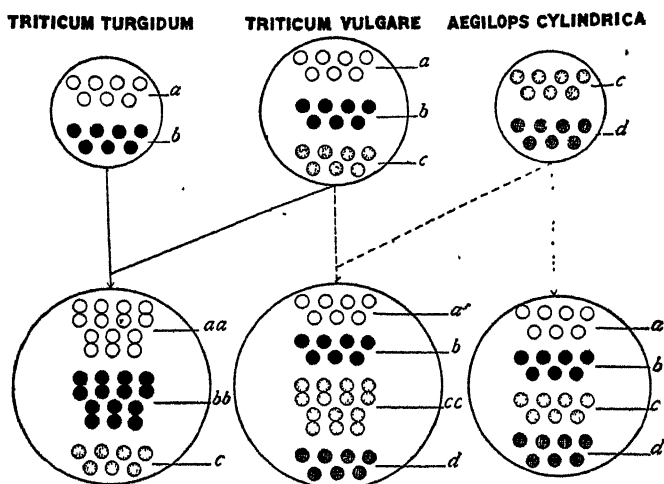


FIG. 28.—Diagram illustrating hypothetical relationships of chromosomes. The 7 chromosomes in set *a* and the 7 chromosomes in set *b* are present in both *Triticum vulgare* (21 chromosomes as the haploid number) and in *T. turgidum* (14 chromosomes). The 7 chromosomes in set *c* are present in *T. vulgare* and in *Aegilops cylindrica* but not in *Triticum turgidum*. The 7 chromosomes in set *d* are present in *Aegilops cylindrica* but not in either *T. vulgare* or *T. turgidum*. A 21-chromosome wheat \times a 14-chromosome wheat gives rise to sporocytes with 14 paired and 7 unpaired chromosomes (lower left). A 21-chromosome wheat \times *Aegilops cylindrica* gives rise to sporocytes with 7 paired and 21 unpaired chromosomes (lower center). *Aegilops cylindrica* \times *Triticum turgidum* gives rise to sporocytes with 28 unpaired chromosomes (lower right).

(var. *pseudo-cervinum* Keke.) characterized by 14 chromosomes, all the 7 chromosomes of *T. monococcum* find synaptic mates. When *T. vulgare* (or other wheat with 21 chromosomes) is crossed with *T. turgidum* (or other wheat with 14 chromosomes), all the 14 chromosomes of *T. turgidum* find synaptic mates (Sax, 1922). When *Triticum vulgare* is crossed with *Aegilops cylindrica*, with 14 chromosomes, only 7 of the *Aegilops* chromosomes find synaptic mates (Text, Fig. 4B; also Sax and Sax, 1924). When *Aegilops* is crossed with *T. turgidum* L. (var. *Plinianum* Keke.), none of the *Aegilops* chromosomes find synaptic mates (research in progress). These facts suggest the hypothesis illustrated by the diagrams in the text (Fig. 28). It is here supposed that the gametes of the 21-chromosome wheats contain three dissimilar sets *a*, *b*, and *c*, of 7 chromosomes each. Two of these sets, *a*

and *b*, are duplicated in *T. turgidum*, and the third set, *c*, is duplicated in *Aegilops cylindrica*, but missing in *T. turgidum*. *Aegilops* and *T. turgidum* have no sets in common. Thus when a 21-chromosome wheat is crossed with *T. turgidum*, the chromosomes in sets *a* and *b* pair, respectively, but the chromosomes in set *c*, finding no synaptic mates, remain unpaired. When the 21-chromosome wheat is crossed with *Aegilops*, the chromosomes in set *c* pair and chromosomes in sets *a* and *b*, lacking synaptic mates, remain unpaired, and for the same reason the chromosomes in set *d* of *Aegilops* remain unpaired. When *Aegilops* is crossed with *T. turgidum*, all the four sets of chromosomes are dissimilar, and hence no homologous mates are present and pairing can not take place.

Thompson (1926) obtained similar results and, in addition, he believes that the 7 chromosomes haploid of rye belong to a different set from those of the *Triticum* and *Aegilops* genera.

Crosses between *Aegilops* and *Triticum*.—Leighty, Sando, and Taylor (1926) have reviewed the literature of *Aegilops* and *Triticum* crosses. They have likewise presented the results of an extensive series of experiments of crosses between species of *Aegilops* with various wheat species. F_1 plants were matured from each cross of *Aegilops* and *Triticum* species (or subspecies). These F_1 plants were highly self-sterile although slight self-fertility was obtained. Backcrosses of the F_1 generic hybrids with wheat were made. These hybrids, often called *A. speltaeformis* by earlier writers, were partially self-fertile. Among the interesting features of *Aegilops*-wheat crosses are the instances of natural hybridization of *Aegilops* and *Triticum*. Percival holds the view that *Triticum vulgare* and its allies may have descended from crosses of *Aegilops* and the so-called *durum* series. It will be remembered that Gaines and Aase (1926) have concluded that *T. vulgare* has two series of 7 chromosome groups homologous with members of the emmer series, that *Aegilops cylindrica* and *T. vulgare* have one series of 7 chromosomes in common and that *Aegilops* and the emmer series have no chromosomes in common. Thus, for example, when *Aegilops* and *T. turgidum* are crossed all four set of chromosomes are dissimilar; no homologous mates are present and pairing cannot take place.

Tschermak and Bleier (1926) have observed several cases of fertile constant breeding hybrids of crosses between *Aegilops ovata* with *T. dicoccoides* and *T. durum*. These resembled the sterile hybrids usually obtained from such crosses. From cytological studies it was decided that they contained 28 pairs of chromosomes which is double the number of the two parents. Tschermak and Bleier believe this lends weight to Percival's view.

Crosses between *T. Durum* and *T. Dicoccum* Wheats with *T. Vulgare*. Varieties of *durum* and *dicoccum* are frequently more resistant to diseases such as black stem rust, caused by *Puccinia graminis tritici* than members of the *vulgare* group. *Durum* wheats also are thought to be more drouth

resistant than varieties of *vulgare*. The question of whether valuable characters of the 14-chromosome group can be combined with the characters and chromosome number of *vulgare* wheat is of much importance in plant breeding. Sax (1923) doubts the possibility that rust resistance can be transferred from varieties of *T. durum* to *T. vulgare* by crossing

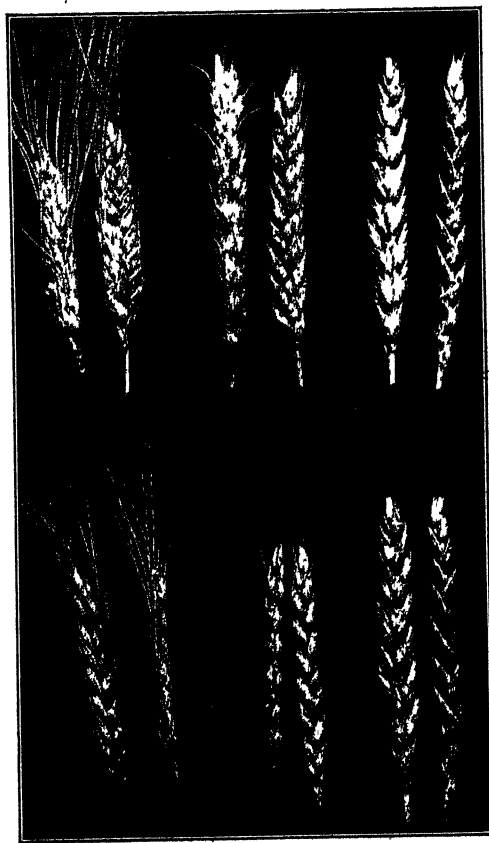


FIG. 29.—Upper group from left to right. Face and side views respectively of Iumillo durum (C. I., 1736), F_1 Iumillo \times Marquis, and Marquis. The F_1 spikes are intermediate in density, have tipped awns and the outer glumes are keeled although not so strongly as Iumillo. Lower group, left to right, face and side views respectively of Emmer, Minn., 1165, F_1 Emmer \times Marquis, and Marquis. The F_1 approaches the Emmer in some spike characters and has tipped awns.

and apparently favors the hypothesis that rust resistance is frequently dependent in species hybrids upon the "physiologic condition of the host." In studies conducted by Sax, accurate correlated data of various morphological characters, chromosome numbers, and rust resistance were taken. The number of plants worked with was small and not extensive enough to warrant a conclusion as to the possibilities of transferring

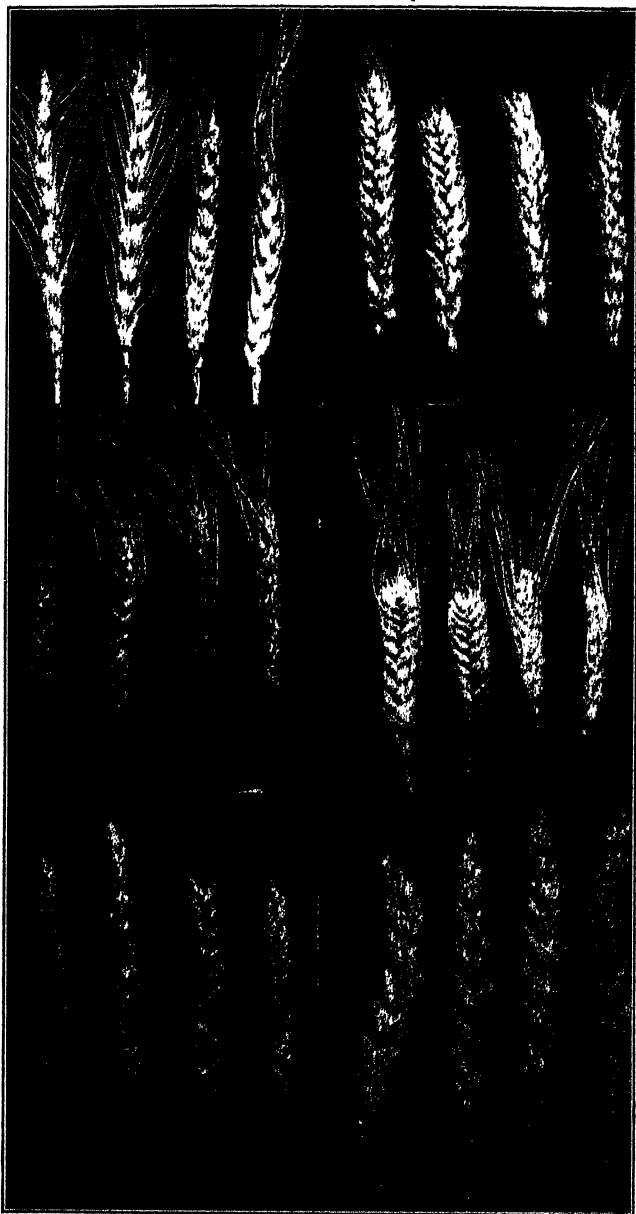


FIG. 30.—Representative spikes of F_2 families of the cross between Durum and Marquis. Upper four groups, F_2 families which were classified as durum. Note that they represent all types of spike density. Lower left, spikes of an awnless F_2 Emmer family. Lower right, four spikes of an F_2 plant which resembled common wheat in spike shape and which proved rust resistant.

characters from *durum* to common wheats. Other characters, moreover, such as grain color, can be transferred from 14-chromosome wheats to the 21-chromosome group and rust resistance and susceptibility are conditioned by genetic factors. Thompson (1925), in a similar study, found that resistance to rust could be transferred from *durum* to common wheats although the common wheat segregates were not as resistant as the *durum* parents. Thompson found that the *vulgare*-like segregates commonly showed one or a few *durum* characters.

Rather extensive studies have been conducted in Minnesota (Hayes and others, 1920, 1925) in attempts to transfer the rust resistance from *durums* to common wheats. From crosses of Marquis, *T. vulgare* × Lumillo, a variety of *T. durum*, a homozygous *vulgare* selection with 21 pairs of chromosomes has been obtained and named Marquillo. This new variety is rather rust resistant although in this respect not the equal of the Lumillo parent. Furthermore, it appears from crosses of this new variety with common susceptible wheats that the rust resistance of Marquillo is dependent upon at least two main genetic factors, these factors having been transferred from Lumillo. This new variety appears about the equal of Marquis in milling and baking qualities although it is rather susceptible to root rot, a character obtained without doubt from its *durum* parent (Hayes and others, 1925).

In a cross between Mindum, *T. durum*, and Velvet chaff, *T. vulgare*, a homozygous segregate which appeared to be a *vulgare* wheat was obtained which was highly resistant in the seedling state in the greenhouse to two physiologic forms of rust to which Mindum was resistant and *vulgare* wheats commonly are susceptible.

McFadden (1925), in South Dakota, has studied large numbers of plants of a cross of a resistant emmer, *T. dicoccum*, and Marquis. Common wheats have been obtained which have proved highly resistant for many years in his plots. One of these was grown in Minnesota in 1925 and proved very highly resistant. From counts made by Griffie they are known to belong to the 21-chromosome group.

These results prove conclusively that rust resistance can be transferred from *durum* and *dicoccum* wheats to the 21-chromosome group.

Inheritance of Milling Quality.—It is generally recognized that milling quality is dependent upon genetic factors but the number and nature of these factors is unknown. Environmental conditions influence the expression of these factors so profoundly that a study of the inheritance of milling quality is almost impossible. Farrer, one of the earliest breeders to study quality, recognized and often stated that milling and baking quality was an heritable character. Various wheat breeders, including Biffin and Engledow (1926) in England, Saunders in Canada, and the Howards in India agree that milling quality is an heritable character. There is every reason to conclude that good milling quality can be com-

bined with other desirable characters by crossing and selection. It was observed both in England and in India that varieties which differed in baking qualities tended to retain their same order of flour strength at different stations. It is a matter of common knowledge that some American varieties of wheat are consistently better in milling and baking qualities than others. Zinn (1923) has analyzed much of the published data of milling and baking quality and of other chemical characters of American wheats. He found a strong correlation between the amount of crude protein in the wheat and in the flour. Loaf volume, as determined by experimental baking trials, was rather highly positively correlated with protein content. While protein content is dependent upon inheritance, environmental conditions strongly influence its development. Clark (1926) has attempted studies of the inheritance of protein content and believes that protein is dependent upon genetic factors as well as environmental conditions. His results serve to emphasize the difficulty of studying the inheritance of such characters.

T. Polonicum Crossed with Other Species.—Crosses between *polonicum* and other forms have been studied. Tscherniak (1913), in a cross between *polonicum* and *vulgare*, explained the results by two main factor differences. The F_1 was of intermediate glume length and in F_2 *polonicum*, *durum*, and *vulgare* forms were obtained as well as intermediates. Pure *polonicum* was considered to contain two dominant factors in the homozygous condition; *durum*, one dominant factor pair in the homozygous condition; and the pure *vulgare* forms, both factors in the recessive condition.

Engledow (1920, 1923) studied the inheritance of glume length in a cross of Polish wheat, *T. polonicum*, with Kubanka, *T. durum*. The ratio for glume length classes in F_2 approximated 1 long:2 intermediates:1 short. The extracted Polish types averaged 20 per cent shorter for glume length than the Polish parent and the *durum* segregates produced somewhat longer glumes than Kubanka. A genetic explanation of this result was not found.

Polonicum (Backhouse, 1918) crossed with *durum* or *turgidum* gave intermediate glume length in F_1 and segregation in F_2 in a ratio of 3 longs and intermediates:1 short. Biffen (1916) and Backhouse in separate studies considered the factor for *polonicum* glume to inhibit chaff pubescence and color. In a cross between *durum* (Kubanka) with a *polonicum* variety, the F_2 segregated for glume length and hairy chaff. The short-glumed plants were in a ratio of 3 hairy:1 smooth, while the long-glumed plants were difficult to classify for condition of chaff. Crosses of different long-glumed plants with other wheats showed that a part of these long-glumed wheats contained a genetic factor for hairy chaff. Results were explained on the hypothesis that the factor for long glume partially inhibited development of hairy chaff. Similar results were obtained by Biffen (1916), for inhibition of glume color by the *polonicum* factor for glume length.

Some Linkage Results in Wheat Crosses.—In crosses between the different species, some evidences of linkage have been observed. In *turgidum-vulgare* crosses, Biffen (1905) obtained complete linkage of gray color of glumes with hairy chaff. Engledow (1914) crossed a black-glumed wheat obtained from a *turgidum*-five cross with a rough-chaffed, white-glumed variety, Essex Rough Chaff. The ratio obtained in F_2 was explained on the basis of repulsion between the factors for black glume color and those for hairy chaff on the 1:3:3:1 series. Kezer and Boyack (1918) obtained complete linkage of black and hairy chaff in a cross of black winter emmer with a smooth,

white-chaffed winter wheat (*T. vulgare*) Freeman (1917) obtained some correlation between a high ratio of width to thickness of spike and hardness of grain in crosses between *T. durum* and *T. vulgare*. He considers, however, that numerous factors are necessary for the development of these characters.

In crosses between members of the 14-chromosome group with members of the *vulgare* group certain characters which differentiate these groups such as grain quality, type of keel of the outer glume, spike density, thickness of neck, etc. tend to be linked although Thompson does not believe the correlation to be absolute.

Nilsson-Leissner (1925) has studied crosses between *T. spelta* and *T. vulgare*. The so-called spelt characters, brittle rachis, 2 to 3 kernal spikelets, thick, blunt, firmly closed outer glumes, prominent veins, and comparatively lax ears appear dependent upon a single gene or a closely linked gene complex. Genes which modify length of internode also effect degree of speling. In the F_2 of the cross between *spelta* and *vulgare*, there appeared to be a linkage between the spelt factor and the factor for awns. The F_2 ratio was as follows: Speltlike awnless, 368 speltlike awned, 153 *vulgare*, awnless, 149 *vulgare*, awned, 36. In F_3 and F_4 similar results were obtained and some lines agreed well with a coupling series while others were in the repulsion phase. The segregation classes agreed well with a crossing-over percentage of 35. Kajanus (1923) obtained similar results.

A fairly definite linkage in wheat has been reported by Gaines and Carstens (1926). The linkage was found in a cross of Velvet Node, a bearded variety with a hairy node, with Hybrid 128, an awnless variety with a smooth node. The calculated crossing-over percentage was 5.2

Spike Density.—Compactness of spike, color of seed and chaff, texture of seed, and presence or absence of awns are frequently used in wheat variety classification.

Nilsson-Ehle (1911b), in crosses between compact and squarehead (middense) wheats, obtained compact forms in F_1 and segregation into compact, middense and lax in F_2 . He explained the results by supposing the main factor differences to be as follows

Swedish Club (compact) $CCL_1L_1L_2L_2$
Squarehead $cccl_1l_1l_2l_2$

The C factor was considered to inhibit the expression of the lengthening factors L_1 and L_2 , and also to produce spikes with short internodes. While these factors gave a satisfactory explanation of his crosses Mayer Gmelin (1917) showed that they did not explain the production of compact-spiked forms which he obtained from crosses of spelt (lax) and Essex Velvet Chaff, which is middense. In F_2 generations grown from individual plants of a cross between white spring emmer and Marquis, studied at the Minnesota Experiment Station, a very common sort of segregation was from lax, keeled, speltlike wheats to compact, keelless, naked wheats. This might indicate that spelt wheats contain a compact factor which is prevented from expression by some other genetic factor.

Crosses between *T. compactum* and *T. vulgare* by Spillman (1909) and Gaines (1917) have shown one main factor difference for compactness. Parker (1914) made careful measurements of internode length in crosses of wheats belonging to *T. compactum* with those of *T. vulgare*. He was able to demonstrate segregation but found the condition very complex. Results of this nature have been satisfactorily explained by the multiple-factor hypothesis. The number of factors involved cannot accurately be determined. Nilsson-Ehle, likewise, states that, besides the main factor differences, there are other minor factors which influence spike density and account for a wide range of homozygous forms.

Stewart (1926) studied crosses of Sevier and Federation, varieties of *T. vulgare*. Sevier is somewhat more dense than Federation. The nature of the F_2 segregation

was determined by studying the F_2 progeny of individual F_2 plants selected at random. Homozygous lax, heterozygous, and homozygous dense forms occurred in the ratio 1:2:1. The dense forms were more dense than Sevier and the lax forms more lax than Federation. Only a very few forms were similar to the parents and no homozygous strains of intermediate density between the parents were observed but the number and nature of the minor modifying factors, if such occurred, were not determined.

Seed Characters.—Color of seed, which results from a brownish, red pigment in one of the bran layers (remains of nucellus) has been quite consistently used in variety classification. This is a plant character and not, therefore, immediately affected by pollination. Red is dominant over white and in the second generation a ratio of 3 red-seeded plants:1 white-seeded plant is often obtained. Nilsson-Ehle (1911b) was the first writer who reported crosses which in F_2 gave 15:1 or 63:1 ratios of red- and white-seeded plants. The Howards (1912), in India, have obtained 63:1 ratios in crosses of American Club with pure lines of Indian wheats, and Gaines (1917) in Washington, has obtained similar results from a cross between Bluestem (red seed) and Brown's Glory (white club wheat). Nilsson-Ehle obtained a ratio of 15 red-seeded plants:1 white-seeded plant from a cross of two red-seeded varieties. The inheritance of this seed color has been explained by one or more Mendelian factors, each when present giving red and when absent white. The factors are separately inherited, each when homozygous producing somewhat darker color than when heterozygous. They are also cumulative, two factors giving a darker color on the average than one of these factors alone. It is impossible, by inspection, to determine how many factors are responsible for a particular varietal seed color.

Harrington (1922) concluded that Kitchener contained two independently inherited factors for grain color, while some strains of Red Bobs and Hard Red Calcutta contained two and others one.

Hayes and Robertson (1924) found that Marquis contained two independently inherited factors for red-grain color and that these were independent in inheritance of the factor for red-grain color carried in Kanred and Minturki winter wheats.

Texture of seed has also been used in varietal classification and is a character which determines to some extent the market class in which the variety will be placed. Biffen (1916) found immediate effect of pollination in a cross of Rivet, a hard-seeded *turgidum* with pollen from a soft Polish variety. The F_1 generation plants produced hard seed and the F_2 segregated into hard- and soft-seeded plants in a ratio of 3:1. The Howards (1915) obtained an intermediate condition in F_1 plants and a 1:2:1 ratio in F_2 in crosses between hard- and soft-seeded strains. Freeman (1918) crossed hard-seeded durum with *T. vulgare*, variety Sonora, a soft-seeded wheat. The F_1 plants produced hard, intermediate, and soft seeds. The hard seeds of the F_1 tended to give more hard-seeded plants in F_2 , and the soft-seeded tended to give more soft-seeded plants. Freeman carried the study through F_4 . He explained his results on the basis of two factors for starchiness, each inherited independently. He supposed each to produce half as much soft starch when heterozygous as when homozygous. As the endosperm is the result of the fusion of two polar nuclei with one of the male generative nuclei, there may be a range of from none to six factors for starchiness of the endosperm. This assumption was shown to explain results quite satisfactorily. The above starchiness is believed by Freeman to be quite different from the well-known "yellow berry" of wheat. Numerous workers have shown that varieties and strains differ widely in the amount of "yellow berry" when grown under the same environmental conditions. Texture of seed is, however, a character which is quite easily modified by unfavorable environmental conditions.

Chaff Characters.—There are a number of different intensities of the chaff color. In some cases a deep brownish-red color is present, in other cases a light brownish-red, and frequently the outer glumes have dark brownish-red striations on a slightly

colored or colorless background Biffen (1905) studied crosses between so-called red and colorless and obtained red or reddish color in F_1 and a 3:1 segregation of colored to colorless in F_2 . Kezer and Boyack (1918), in winter-wheat crosses in which the parents differed in chaff color, obtained intermediate color in F_1 and segregation in a 3:1 ratio in F_2 . Simple ratios in varietal crosses have been reported by others for this color character. As there are different intensities which are quite uniform in inheritance, it seems reasonable to conclude that there are different factors in different varieties for brownish-red color. In a *durum-vulgare* cross, Love and Craig (1918a) obtained in F_2 an indication of a 15.1 ratio for brownish-red and colorless chaff.

Besides the chaff colors there are awn colors. The Howards (1915), in India, obtained a ratio in F_2 of 3 45 black-awned:1 colorless in a cross between Indian wheats.

Hairy chaff is a varietal character of considerable classification value. The Howards have made extensive studies of this character. Under linkage relations a number of cases were given in which hairy chaff was correlated with glume color. Henkemeyer (1915) reports different crosses, one in which hairy chaff is correlated with white chaff and another in which these characters are independently inherited. This leads one to suspect that there are two kinds, either of hairy chaff or of chaff color. The Howards have been able to demonstrate two kinds of hairs on the glumes of Rivet wheat. Two Indian varieties were likewise studied. Each produced hairy chaff, but differed in the sort of hairs produced. In crosses between these varieties, ratios of 15 pubescent:1 smooth were obtained in F_2 .

Presence or Absence of Beards.—Wheats have been classified as bearded and awnless but this is not genetically correct. The awn is an extension of the flowering glume. The common wheats, like Marquis and Bluestem, are not truly awnless for there is a short extension of the awn particularly in the spikelets at the top of the spike. Ratios of 3:1 have been obtained generally in crosses between bearded and so-called awnless (tip-awned) wheats. The Howards (1915) explained the inheritance of these characters by supposing two factors, *A* and *B*, to be present in a homozygous condition in bearded wheats. They have found two kinds of very short-awned wheats, one like the tip-awned Marquis or Bluestem, and the other with somewhat longer tip awns. Each of these varieties was found to contain one of the factors *A* or *B* in a homozygous condition. In crossing a tip-awned wheat like Marquis with bearded varieties, the F_1 generation, as a rule, shows an extension of the tip awns and it is frequently possible to separate these F_1 plants from the tip-awned parent. In crossing bearded with true beardless, the F_1 is apparently beardless and there is a range in F_2 from completely bearded to awnless. Fully bearded plants breed true for this character.

Other workers have used a two-factor hypothesis to explain the segregation in crosses between awnless and bearded varieties. In some cases it is believed that there are modifying factors which affect the expression of the main factors (Clark, 1926) Stewart explained his results by supposing that the two main factors for beards were linked. It is apparent that the inheritance of presence and absence of awns and of intermediate types is more complex than it was thought to be formerly and further study of the problem is necessary.

Inheritance of Disease Resistance.—Biffen (1907a, 1912, and 1917) has found that the inheritance of host reaction to stripe rust, *Puccinia glumarum*, is a simple Mendelian character. Susceptibility is dominant over resistance and in F_2 , ratios of 3 susceptible:1 resistant are obtained. Nilsson-Ehle (1911b) in a similar study found the F_1 generation resembled the susceptible parent in some cases, the resistant in others, and was intermediate in still others. Complex segregation for resistant *versus* susceptible forms was obtained in later generations. Results were explained on the multiple-factor basis. Armstrong (1922) found that the F_1 of a cross of a resistant and susceptible variety was of an intermediate nature. Resistance and susceptibility appeared to be dependent upon a single-factor pair although genetic factors for other

plant characters apparently modified the expression of the factors for resistance and susceptibility.

Studies by Stakman and others (1919-1922) have shown the probable reason for conflicting reports regarding inheritance of resistance to black stem rust of wheat, *Puccinia graminis tritici*. They have demonstrated the fact that there are a number of physiological or racial forms of rust roughly analogous to pure lines. These forms can be differentiated only by their specific reaction to pure-line wheat varieties. Studies of their constancy indicate that they are not easily modified, *i.e.*, that the parasitic reaction of each form is constant. As has been noted it appears possible to transfer the rust resistance of *T. durum* and *T. dicoccum* to *T. vulgare* by suitable crosses. •

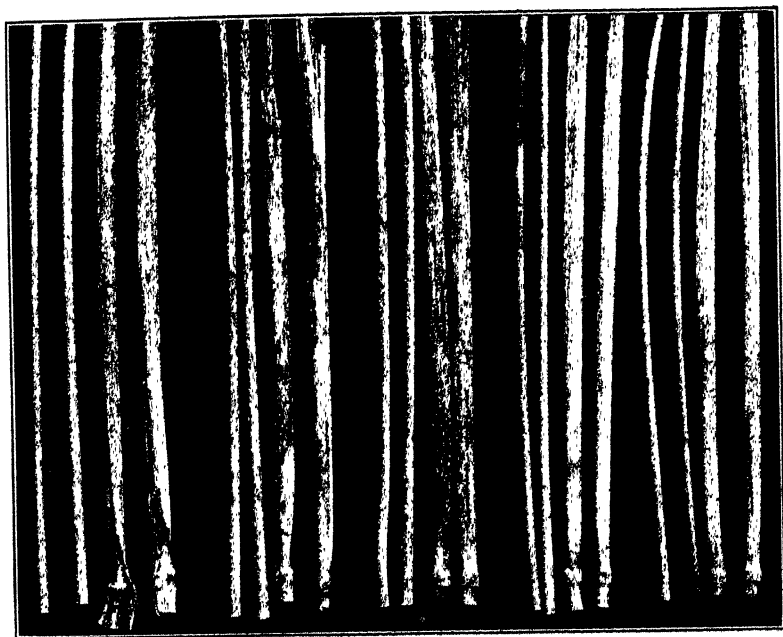


FIG. 31.—Resistance of parents and crosses to a strain of stem rust. From left to right: Culms of resistant Durum wheat; F_1 of Durum \times Marquis, susceptible; Marquis, susceptible; F_1 of Emmer, Minn. 1165 \times Marquis, as resistant as the Durum varieties; Emmer, Minn. 1165, a very resistant variety.

As there are many physiologic races of rust which can be differentiated only on the basis of their reaction upon particular wheat varieties, it seems reasonable to expect numerous genetic factors which condition resistance and susceptibility. In some cases resistance and immunity are dominant to susceptibility and in other crosses susceptibility has been found to be dominant to resistance.

Several crosses have been carefully studied where the parents reacted in a reciprocal manner to two physiologic races of rust. These comprise crosses of *durum* \times *vulgare*, *durum* \times *durum*, and *vulgare* \times *vulgare*. In each case varieties were obtained which contained factors for resistance or immunity to both rust forms and other varieties which were susceptible to both (Puttick, 1921; Harrington and Aamodt, 1923; Hayes and Aamodt, 1923).

There are two sorts of resistant varieties. Some varieties are highly resistant in the greenhouse in the seedling state and these varieties, when mature, are resistant to the same physiologic forms of rust under field conditions. Some varieties, however, are rather susceptible in the seedling state in the greenhouse to certain physiologic forms but they may be highly resistant to these same forms under field conditions when approaching maturity. The resistance in the seedling state is believed to be physiologic in nature, while there is some evidence that the resistance of plants when approaching maturity is dependent upon morphologic characters (Hursh, 1924).

Kanred, a winter-wheat variety of the Crimean group, is immune from 11 physiologic forms of rust and highly resistant to 9 others. The immunity of Kanred is a dominant character in crosses and dependent upon a single factor pair (Aamodt, 1923). If resistance to several physiologic races is controlled by a single genetic factor, the problem is simplified greatly (Hayes and Stakman, 1922).

There is some evidence that the field resistance of Marquillo (the 21-chromosome segregate, from the cross of Iumillo and Marquis) to many and perhaps all physiologic forms is dependent upon two main pairs of factors and that these are independent in inheritance of the factor for immunity carried by Kanred. The resistance of Marquillo and of Kota (the rust-resistant variety of *T. vulgare* produced from a plant selection at the North Dakota Station), moreover, appears to be dependent upon different factors since F_2 crosses of Kota \times Marquillo are preponderantly susceptible although resistant types can be recovered.

Gaines (1918, 1920, 1923, 1925), Gaines and Singleton (1926), and Briggs (1926) have studied the inheritance of resistance of wheats to bunt or covered smut caused by *Tilletia tritici*. The method used in studying bunt resistance was to blacken the seed with smut spores just before planting and study the individual crosses and strains in the segregating generations by the individual-plant method. Some wheats such as Martin, Hussar, and White Odessa are bunt free and are considered immune. Turkey and Florence are highly resistant. Forty Fold and Red Russian are slightly resistant. Most bread wheats are susceptible. Crosses between susceptible varieties have given only susceptible offspring while crosses between resistant varieties have shown transgressive segregation and from such crosses lines have been obtained which bred true for either immunity, resistance, or susceptibility.

Susceptibility is generally dominant to resistance while crosses of the immune with the susceptible are resistant in F_1 . Gaines has studied over 25 separate crosses and explains the results obtained in each on a multiple-factor basis. On the other hand Briggs explained the results of one cross between immune and susceptible varieties by a single dominant factor for immunity.

Spring versus Winter Habit.—Various investigators have studied the inheritance of spring *versus* winter habit of growth. True winter wheats, when planted in the spring, fail to head, as a rule, although in northern climates, where the day is long, they may shoot late in the season. Recent investigators of the mode of inheritance of spring *versus* winter habit of growth have found that spring habit is a dominant character. Cooper (1923) explained the results of two crosses of spring *versus* winter wheats on a monohybrid and dihybrid basis, respectively, while Nilsson-Leissner (1925) obtained an approximation to a 15:1 ratio of spring *versus* winter types in F_2 . Vavilov and Kouznetzov (1921) and Aamodt (1923) obtained a complicated segregation in F_2 and later generations and were not able to explain their results on any simple factor basis.

Spring wheats in general are less winter hardy than true winter wheats although some spring wheats, when they are planted in the fall, are much more resistant to winter injury than others. Winter hardiness and cold resistance are not necessarily the same thing. For example, winter wheats which are most hardy in Minnesota do not excel in winter hardiness in West Virginia. It is believed that these wheats are cold resistant but are injured by other causes in West Virginia.

Inheritance of Other Characters.—Nilsson-Ehle (1911c, 1912) has shown that winter hardiness is inherited in much the same manner as other characters. Segregation occurs in F_2 and types can be produced in later generations which are homozygous for different degrees of winter hardiness. Crosses made (Hayes and Garber, 1919) in 1902 between hardy Odessa winter wheat and Turkey varieties were bred for several years by continuous selection methods. Odessa is a late-maturing variety and does not give a high yield in Minnesota. Turkey is a desirable winter wheat in many sections but it lacks hardiness under Minnesota conditions. Two early maturing wheats when grown in Minnesota, Minhardi and Minturki, have been produced from the cross between Turkey and Odessa. These new varieties excel in winter hardiness and yield.

Earliness in Wheat.—Several investigators have studied heading and ripening periods in wheat crosses. Thompson (1918) found that the F_1 generation was about as late in maturity as the later parent. Crosses were studied between many pairs of wheat varieties differing by many degrees in period of heading and ripening. Each F_2 generation formed regular curves of probability with intermediate means. The multiple-factor hypothesis explained the results satisfactorily when each cross was considered separately but when all combinations of crosses were considered together the results were not so easily explained genetically. Florell (1924) states that other workers have found an intermediate period of ripening in F_1 but inclined toward one or the other parent. Florell placed his F_2 generation in a large early group and a smaller late group in the ratio of 3.07:0.93 which indicates one allelomorph pair of factors. In some cases, however, more complex segregations were obtained. Clark (1926), in crosses of Marquis and Hard Federation, found that early heading was dominant to late heading but he was unable to place his results in the segregating generation on a definite factor basis. Thompson found that earliness could be combined with other desirable qualities by Mendelian methods although it was necessary to raise large numbers of plants as the majority were of intermediate habit.

Dwarfs in Wheat.—The mode of inheritance of dwarfs in wheat has been studied by several investigators. In some cases the results have been placed on a definite genetic basis and they have approximated 3:1 or 13:3 ratios depending upon the number of factors involved. In one two-factor hypothesis, D is a dominant dwarf factor which, when present, produces dwarfs except in the presence of I , an inhibitor which always leads to the production of normals. The progeny of plants heterozygous for both I and D segregate in a ratio of 13 normals:3 dwarfs. When D is homozygous and I heterozygous, a ratio of 3 normals:1 dwarf is obtained. When I is absent and D heterozygous, dwarfs result and segregation in later generations of 3 dwarfs:1 normal may be expected. Waldron (1924) obtained ratios approximating 55:9, 15:1, and 63:1 for normals and dwarfs in F_3 generations of a Kota-Marquis cross. He explains these results by supposing the genes concerned to be in an extremely labile condition often changing from dwarf genes to normal and *vice versa*. Goulden (1926) has studied similar material. By a combined genetic and cytologic mode of attack, higher ratios such as 15:1 and 63:1, were explained by supposing that as a result of irregular pairing of the chromosomes, trivalents and lagging chromosomes might result which would modify ratios. This sort of explanation was first advanced by Winge (1924) to account for aberrant ratios obtained in studies of speltoid heterozygotes.

Speltoid and Other Complex Types in Wheat.—Nilsson-Ehle (1920, 1921), Akerman (1920, 1923), Lindhard (1922, 1923), Kajanus (1923), Winge (1924), and others have studied various types of abnormalities in wheat with special attention to speltoid types. Nilsson-Ehle thought that the so-called speltoid mutations formed a set of multiple allelomorphs—normal type, bearded speltoids, and beardless speltoids. Akerman observed speltlike bud sports in wheat which often affected parts of a spike. In some cases these abnormalities were inherited while in other cases it appeared

that the speltoid character affected only the epidermis and the germ cells transmitted only normal characters. Deviations from the normal ratio of 1 normal 2 heterozygous 1 speltoid were common. These were explained by the elimination of certain gametes, by heterogamy, *i. e.*, the unequal distribution of the members of an allelomorphic pair to the functioning ovules and pollen and by linkage. As has been mentioned Winge explains certain deviations through cytological irregularities.

CHAPTER XI

CLASSIFICATION AND INHERITANCE OF SMALL GRAINS OTHER THAN WHEAT

In the cases of barley and oats quite usable classifications have been proposed. The general adoption of such classification schemes is desirable for often great confusion results from the incorrect use of varietal names. Classification schemes cannot be given in detail in a plant-breeding text. It seems sufficient here to point out the genetic relationship between wild and cultivated species and to give the major so-called species groups for the various crops. The more important botanical and agronomic characters which are commonly used in varietal classification have also been mentioned. As crossing must frequently be resorted to as a means of improving small grains, the student should have a working knowledge of the known facts of inheritance with respect to particular characters.

CLASSIFICATION AND INHERITANCE IN OATS

A workable classification of cultivated American oat varieties and the basic wild species has been made by Etheridge (1916). The following outline of species groups is taken from his publication:

- A. Kernel loose within the surrounding hull; lemma and glumes alike in texture.
Avena nuda.
- AA. Kernel firmly clasped by the hull; lemma and glumes different in texture.
 - B. Upper grains persistent to their rachillas.....*Avena byzantina.*
Avena sterilis.
 - BB. Upper grains easily separating from their rachillas.
 - C. Lemma extending as teeth or awn points.
 - D. Lemma with four teeth or awn points.....*Avena abyssinica.*
 - DD. Lemma with two teeth or awn points.
 - E. Lemma elongate, lanceolate, with distinct awn points.
Avena strigosa.
 - EE. Lemma short, abrupt, blunt, rather toothed than awn-pointed.....*Avena brevis.*
 - CC. Lemma without teeth or awn points.
 - D. Basilar connections of the grains articulate...*Avena fatua.*
 - DD. Basilar connections of the grains solidified.
 - E. Panicles roughly equilateral, spreading...*Avena sativa.*
 - EE. Panicles, unilateral appressed...*Avena sativa orientalis.*

Chromosome Numbers in Oats.—Various investigators have studied chromosome numbers in oats. Kihara (1919) found the following haploid numbers: (1) 7, *Avena strigosa*; 14, *A. barbata*; 21, *A. fatua*, *A. sativa*, *A. sterilis*, *A. byzantina*. Huskins (1926) presents the following counts: 7, *A. brevis*, *A. strigosa*; 14, *A. barbata*, 21, *A. sterilis* and *A. nuda*. Aase and Powers (1926) report haploid numbers of 7 in *A. brevis* and *A. strigosa* and 21 in *A. sativa*, while Goulden (1926) reports *A. sativa*, *A. fatua*, *A. sterilis*, *A. nuda* with 21 as a haploid number and *A. brevis*, *A. barbata*, and *A. strigosa* with a haploid number of 7. It is of interest that 7-, 14-, and 21-haploid chromosome groups are found in oats as in wheat.

Crosses between *Avena Fatua* and *A. Sativa*.—It is generally accepted that *fatua* is the stem species from which *A. sativa* and *A. sativa orientalis* originated. Tschermak (1914) has made extensive crosses and obtained nearly complete fertility in crosses between *fatua* and *sativa* forms. Surface (1916) has found a number of characters which in crosses between *fatua* and *sativa* are associated with the *fatua* base: (1) heavy awn on lower grain, (2) awn on upper grain, (3) *fatua* base on upper grain, (4) pubescence on rachilla of lower and upper grain (5) pubescence on all sides of the base of lower grain and pubescence on the upper grain.

Origin of Cultivated Varieties of *A. Byzantina*—Coffin, Parker, and Quisenberry (1926) have adopted the use of the name *A. byzantina* for the cultivated varieties of oats which presumably descended from the wild form of *A. sterilis*. This is the terminology favored by European workers. They point out that there is a great deal of variation in such varieties as Burt and Fulghum which belong to this group and quote Schultz who observed that some cultivated forms of this group resembled *A. sterilis* rather closely while others can scarcely be distinguished from *A. sativa*. Salmon and Parker (1921) suggest that Fulghum may have resulted from a natural cross of *A. sativa* and *A. sterilis* forms. As some cultivated forms of this group differ so widely from wild forms of *A. sterilis* it seems desirable to adopt the specific name, *A. byzantina*, for this group.

Norton (1907) pointed out that the red oats grown in southern United States without doubt descended from *A. sterilis* of the Mediterranean region. Trabut (1914) gives convincing evidence that the cultivated oats of the Mediterranean region have been obtained from a wild *A. sterilis*, which is still quite common. It is of interest that the cultivated oats grown in the warmer regions of the United States descended from warm-climate ancestors. The value of this group of oats for the southern United States has been shown clearly by Warburton (1914).

Breeding Oats for Particular Regions.—It is apparent that the cultivated varieties of *A. byzantina* are superior in the warmer regions, such as the southern United States, to the cultivated varieties of *A. sativa*. Arrhenius (1924), in discussing the gray-spot disease of oats which is prevalent in Holland and Sweden, states that the use of resistant varieties

is one means of controlling the trouble. The disease is characterized by the spotting of young leaves at the base, the later breaking and withering of the leaves at the diseased places, and the failure in some cases of normal fruiting. The disease is non-pathogenic and results from undue proportions of lime in the soil.

In a study of yielding capacity of oats conducted at the Welsh Plant Breeding Station (Jones, 1923), it was learned that one group of varieties succeeded better on land of high-producing capacity while a different group yielded better on land of low-producing capacity. In breeding oats and other small grains disease resistance is an important character.

Disease Resistance in Oats.—Stem and crown rust, caused by *Puccinia graminis avenae* Erikss. and Henn., and *Puccinia coronata* Corda, respectively, and the smuts *Ustilago avenae* (Pers.) Jens. and *U. levis* (K. and S.) Magn. are among the most destructive parasites of oats. Parker (1918) and Durell and Parker (1920) studied varietal resistance to both rusts, while Stakman, Levine, and Bailey (1923), and Mackie and Allen (1924) studied reaction to stem rust. Heald (1919), Reed (1920), and Sampson and Davies (1923) made studies of varietal susceptibility to smuts. Resistant varieties have been obtained and some of the best of these have been used in breeding experiments.

Stakman, Levine, and Bailey (1923) and Reed (1924) observed instances of physiological specialization in stem rust and smuts, respectively, of oats. Reed found, however, that certain varieties appeared resistant to all the races of smuts which he used. These varieties were Black Mesdag, Fulghum, and Red Algerian. In Iowa, Durell and Parker found that Green Russian, Ruakura, and *A. barbata* were resistant to both crown and stem rust. White Tartar (White Russian), while susceptible to a form of stem rust obtained from Sweden, has proved highly resistant in the United States.

Studies of the inheritance of resistance to crown rust under greenhouse conditions in crosses of Burt with Sixty Day, *A. sativa*, showed segregation in F_2 . Susceptible and resistant plants, as well as various intermediates, were obtained (Parker, 1920).

A study of the inheritance of resistance to stem rust has been made at the Minnesota Station (Garber, 1922a). F_1 , F_2 , and F_3 crosses of resistant White Russian with two susceptible varieties of *A. sativa*, Victory and Minota, have been grown. The results show that for these crosses resistance is a dominant character, the ratio in F_2 of resistant and susceptible plants approximating 3:1. Susceptible F_2 plants bred true to susceptibility in F_3 , while resistant F_2 plants were of two kinds: (1) those which produced only resistant progeny and (2) those which segregated, both resistant and susceptible plants being obtained.

Griffie (1922) found that resistance to stem rust can be studied advantageously under greenhouse conditions by inoculating several

seedling plants of each selection. In this manner, it is possible to obtain lines in F_3 which are homozygous for resistance.

Studies on the inheritance of reaction to loose and covered smuts have been made. Wakabayashi (1921) studied the reaction to covered smut of a cross of Red Rustproof with Black Tartarian. The Red Rustproof was immune from attacks of *Ustilago levis* while Black Tartarian was rather susceptible. Resistance proved a dominant character. Apparently several factors were involved as only 12 families in F_3 out of 95 produced any smutted plants. Gaines (1925) studied crosses of Red Rustproof with several other varieties and obtained results similar to those of Wakabayashi. Barney (1924) also studied reaction to loose smut and concluded that the results for the three crosses could be explained on a monohybrid, dihybrid, and trihybrid basis, respectively. Reed and Stanton (1925), in crosses of Fulghum which is resistant to both forms of smut with Swedish Select which is susceptible, obtained 25 families in F_3 out of 92 which were as resistant to both forms of smut as Fulghum. Resistance to both forms appeared to be dependent upon the same genetic factors. Correlation studies of the reaction to smut and of other characters in which the parents of the crosses differed led to the conclusion that it was possible to combine smut resistance with other morphological characters. Studies conducted at Minnesota indicate that susceptibility and resistance to stem rust are independent in inheritance of reaction to smut. In these studies Black Mesdag was used as the smut immune parent while rust resistance was obtained from White Russian.

Differences in Awn Development.—Varieties of oats differ in the presence or absence of awns and in the degree of awn development. Nilsson-Ehle (1911a) first used the hypothesis that the yellow gene inhibited the development of awns. This hypothesis was substantiated by careful experiments. A number of crosses between *Avena fatua*, hairy awns on both grains, with early oats belonging to the *Avena sativa* group have been studied. Using Sixty Day with yellow grains as the awnless parent, Love and Craig (1918c) observed the F_1 to have the lower grain often awned but the upper grain awnless. They concluded that the yellow factor inhibited the complete development of awns. In a similar cross, Surface (1916) obtained like results in F_1 and concluded that one main factor difference was necessary to explain the results. Modifying factors were involved which affected the degree of development of awns. No significant evidence was found that the yellow gene inhibited the development of awns.

FIG. 32.

- 1 Branch of oat panicle.
- 2 Spikelet, showing tertiary floret just after blooming—*a*, primary floret.
- 3 Spikelet, showing flower parts—*a*, outer glume; *b*, flowering glume; *c*, palea; *d*, lodicules; *e*, anther; *f*, stigma; *g*, secondary floret; *h*, awn.
- 4 Outer parts removed, showing sexual organs.
- 5 Longitudinal section ovary.
- 6 Anther.
- 7 Showing outer and flowering glume of lower spikelet removed—*a*, lodicules, and sexual organs.

Size: 1, 2, about n ; 3, about $2n$; 4, 5, 6, greatly enlarged, 7, about $2n$.

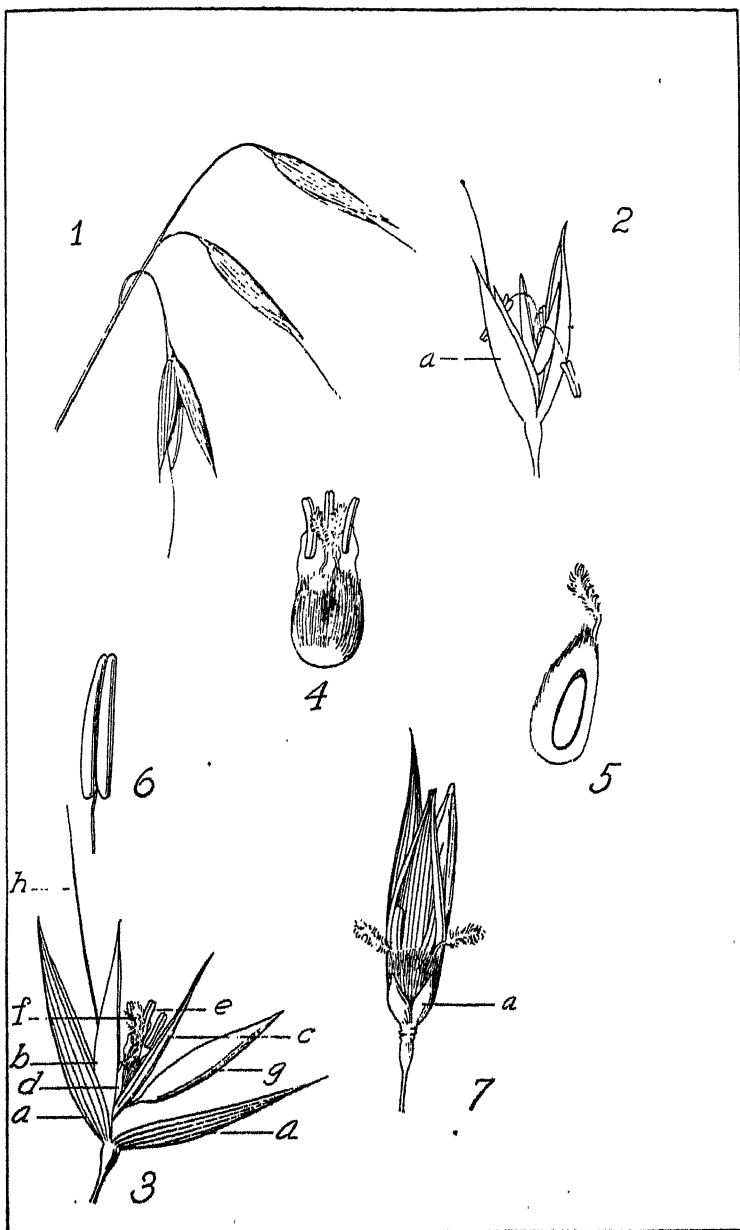


FIG. 32.—For description see opposite page.

Fraser (1919) has studied a cross between an awnless Sixty Day and Burt, the latter being a variety of the *Avena byzantina* group. The Sixty Day parent produced bright-yellow grains with no awns. The Burt parent usually produced awns on the lower grains and frequently on the upper but they show weak development. Fraser classified awns as strong, intermediate, and weak. The strong awn is twisted at the base and has a sharp bend about three-eighths of the way from the base to the tip. It is also stiff and long. The intermediate awn lacks the bend of the strong awn and is less stiff. It is generally twisted at the base and is often curved. The weak awns vary greatly from almost imperceptible structures to weakly developed ones. The F_1 plants of Burt \times Sixty Day were practically awnless. In F_2 there was a ratio of fully awned (awned like Burt or with awns more completely developed) to awnless and partly awned of 1:3. The fully awned bred true in later generations. Results substantiated the hypothesis that Sixty Day carried a factor for awning which was inhibited from development by the yellow factor.

Color of Grain and Straw.—Color of the lemma when ripe is a character which is easily affected by environment. Weather conditions at ripening are important and greatly modify the expression of inheritance of these color characters. With bright sunshine a deeper color is developed than in wet, cloudy weather. Black- or yellow-grained varieties under unfavorable environmental conditions are much less intensely colored. The stage of maturity at which the grain is harvested or weathering after harvesting may also modify these color characters.

The color of the lemma of oats has been classified as black, brownish-red, gray, yellow, and white. Different varieties, likewise, exhibit different intensities in the development of a particular color. In some crosses between black and white a ratio of 15 blacks:1 white was obtained in F_2 (Nilsson-Ehle, 1909), while the majority of crosses show 3:1 ratios (Nilsson-Ehle, 1909), (Games, 1917). The simplest explanation is that each color character is due to one or more factors, each factor when heterozygous causing partial or complete development of the character.

Results of crosses show that yellow is dominant over white or partially so. There are, however, two yellow factors, each independently inherited. In a cross between Burt, which produces yellowish-red seeds, and Sixty Day, which produces yellow seeds, Fraser (1919) obtained a ratio of 48 red:15 yellow:1 white in F_2 . These results may be explained by supposing Burt to carry two color factors, R for red and Y for yellow, and Sixty Day one factor, Y^1 for yellow. Apparently R produces reds either when associated with Y or Y^1 or when alone.

Gray is epistatic to yellow (Nilsson-Ehle, 1909); Surface, 1916; Love and Craig, 1918c) but hypostatic to black, while black is epistatic to all other colors so far as determined. It has been tested for gray, yellow, and white but not for brownish red. As a rule the intensity of color is not so great when a factor for a particular color is heterozygous as when homozygous.

The inheritance of a reddish straw color has been shown by Pridham (1916) to behave as a simple Mendelian monohybrid.

Hulled versus Hull-less.—The hull-less condition has been made the basis of one of the species groups, *Avena nuda*. Numerous crosses between hulled and hull-less forms have given like results. All investigators of these crosses have obtained an intermediate condition in F_1 , with both kinds of grains, hulled and hull-less, borne in the same panicle. Ratios in F_2 of 1 of each of the hulled and hull-less forms:2 heterozygotes have been obtained. The hulled and hull-less types breed true while the intermediates again segregate. Love and McRostie (1919) have found considerable variation in the percentage of hulled and hull-less seeds in different panicles of the same cross. Consistent correlation was obtained between the percentage of hulled grains on heterozygous F_2 plants and that of hulled grains on heterozygous F_2 plants of the progeny. Some heterozygous F_2 plants with low percentages of hulled grains

gave heterozygous progeny with correspondingly low percentages. A similar behavior was obtained in the progeny of heterozygous plants with high percentages of hulled grains, while plants with intermediate percentages of hulled grains gave heterozygous progeny with low, intermediate, and high percentages in different plants. This suggests the presence of a factor which affects the percentage of hulled and hull-less grains of heterozygous plants.

Chinese Hull-less produces colorless floral glumes but carries a brownish color in the palea. When crossed with hulled varieties it transmits a factor for black color which in the presence of the homozygous condition for hulled leads to the development of dark color in both floral glumes and palea. Gaines (1917) concluded that the naked condition inhibited the development of black in the floral glumes in the Chinese Hull-less variety.

Pubescence.—Cultivated varieties of oats differ in the amount and in the presence and absence of basal hairs on each side of the callus. In some crosses only one factor is involved, in others two factors. In some crosses between parents which have different degrees of pubescence there is an increase in the number of basal hairs, and forms are obtained in F_2 which have more pubescence than either parent, likewise forms which lack pubescence. Certain wild forms of *Avena fatua* carry two independently inherited factors for pubescence (see Surface, 1916; Zinn and Surface, 1917; Nilsson-Ehle, 1908; Love and Craig, 1918c).

Characters of Base of Lower Grain.—In wild forms of *Avena fatua* and cultivated forms of *Avena byzantina* there is a distinct articulation at the base of the lower grain. According to Surface (1916) this causes wild oats to shatter while in cultivated races of *sativa* the grains are not easily separated from their base and do not ordinarily shatter. The F_1 generation of a cross between *A. fatua* and Kherson was intermediate as regards the base of the lower grain, but nearer the cultivated form, while the upper grain had a base similar to the cultivated parent. Segregation in F_2 gave a ratio of wild, intermediate, and cultivated of 1:2:1. This leads to the assumption of a single factor difference which separates cultivated and wild in the form of the base. As has been mentioned, there is strong association of many other characters and the wild form of the base. Love and Craig (1918c) found an indication of a single factor difference for the presence and absence of basal articulation but found that the yellow factor inhibited the development of the wild or articulated base.

Avena byzantina differs from other oat species in having the upper grain persistent to the rachilla. The base of the lower grain resembles *A. fatua* in its articulation. In crosses between Burt, belonging to *A. byzantina*, and Sixty Day, the F_1 was intermediate and in F_2 the Burt, or sterilis type, of articulation at the base of the lower grain could be determined accurately. Ratios approximating 1 of the Burt type:3 of the intermediate and *sativa* types were obtained (Fraser, 1919). It should be remembered that Burt oats is a very variable type and that the results given here are in relation to the particular strain of Burt used by Fraser.

Open versus Side Panicle.—Nilsson (1901) has used panicle types and seed colors as a chief means of classification. The distinction between the side and the open panicle is easily made, but the various transitional open-panicled forms are not easily used in differentiation. Nilsson-Ehle (1908) has explained crosses between an open- and a side-panicled variety on the basis of two main factor differences. Either factor when homozygous or heterozygous produces open panicles. When both factors are homozygous a variety with an open panicle and drooping branches is obtained. When the factors are absent a side panicle results. From crossing two open-panicled forms, nine-side forms were obtained out of a total of 112 plants. These side-panicled plants bred true while of the 103 open-panicled plants, 24 again segregated giving both open- and side-panicled forms. The parental varieties have panicles with erect branches while a part of the open-panicled segregates have drooping branches.

Gaines (1917) and Garber (1922) found considerable difficulty in separating open- and side-panicked types of the segregating generations. The correct genetic explanation for the variations which occurred was not learned.

Size Characters.—Nilsson-Ehle (1908) made numerous studies of inheritance of size characters. In a cross between two *sativa* varieties which differ in height, transgressive segregation occurred in F_2 . Forms were selected and the studies continued through F_4 and F_5 . Segregation was of a complex nature. Transgressive segregation also occurred in crosses involving leaf breadth, kernel size, and number of florets to the spikelet. The results were explained on the multiple-factor hypothesis, but the

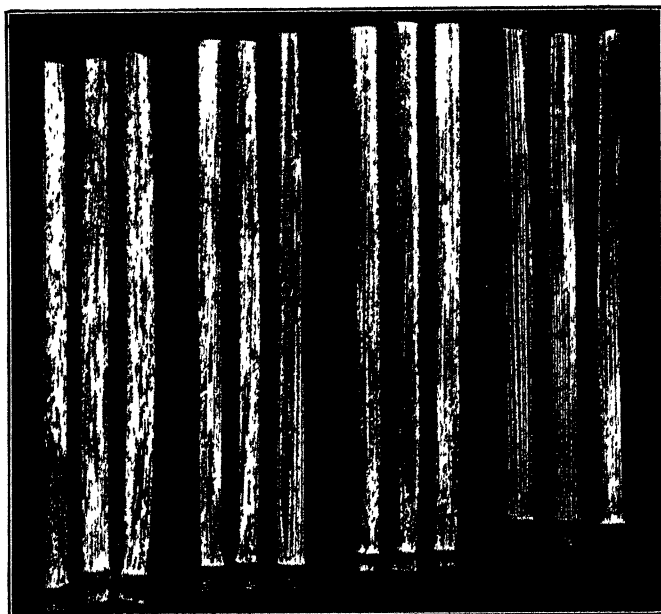


FIG. 33.—Culms of resistant and susceptible varieties of oats. From left to right: Victory, susceptible to stem rust; a susceptible F_2 plant of Victory \times White Russian; a resistant F_2 plant of Victory \times White Russian; resistant White Russian.

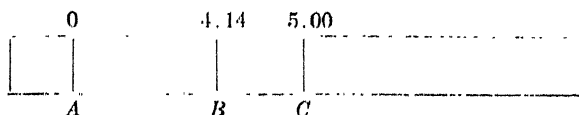
actual factors involved could not easily be determined. Maturity may be considered under this heading, for it behaves in a similar manner. From crossing early and later maturing oats, Caporn (1918) obtained intermediate maturity in F_1 and segregation in F_2 . The author suggests that three factors will quite satisfactorily explain the results. Nilsson-Ehle obtained transgressive segregation in F_2 in a cross between medium early and late-maturing varieties. Progeny from 112 F_2 plants were grown in F_3 . Of these 112 plants 4 gave progenies earlier than the early parent and 10 later than the late parent. Many of the remaining 98 plants produced progenies that segregated for maturity. Noll (1925) studied period of maturity in several oat crosses. He explained his results due to a series of dominant factors for earliness which together had a cumulative effect.

Garber and Quisenberry (1927) studied the mode of inheritance of date of heading, leaf width, number of culms, and color of seed. Earliness was found

to be inherited as a dominant character and dependent upon at least two factors. Leaf width was very variable and strongly influenced by environmental conditions. Segregation occurred in F_2 and one F_3 family had a lower mean leaf width than Gopher, the narrow-leaved parent. Number of culms is an inherited character and strongly influenced by environmental conditions. Black was dominant over white and dependent upon a single factor. No positive evidence of close linkage of any of the characters studied was obtained.

Linkage of Characters.—Association of numerous characters in inheritance has been mentioned in the discussion of crosses between the wild *A. fatua* and cultivated varieties of *A. sativa*. Aside from the general characters mentioned, linkage has been found between the factor for black color of the lemma and one of the factors for pubescence.

In crosses between Burt, *A. hyzantinina*, and Sixty Day, *A. sativa*, Fraser (1919) has found that the factors for the articulated base of the lower grain, the awned condition, and the production of medium basal hairs were linked in inheritance. In the following diagram *A* represents the factor for awning, *B* for Burt base, and *C* a factor for the production of medium basal hairs.



The percentages of cross-overs were determined for F_2 and F_3 . As has been pointed out segregation for awns, basal hairs, and type of base was on a monohybrid basis in each case. Five per cent of cross-overs occurred between the factors for awning and basal hairs; 4.14 per cent between awning and the factor for Burt base, and 1.79 per cent between Burt base and basal hairs.

Odland (1927) studied rachilla length in a cross between the varieties Early Gothland, long rachilla, with Garton 784, short rachilla. The length of rachilla was found to be little modified by ordinary environmental conditions. Homozygous lines for various rachilla lengths were obtained in F_3 and F_4 . Multiple factors were used to explain the mode of inheritance and there was a close linkage between one factor pair or group of factors for length of rachilla and the factor pair controlling pubescence of rachilla.

False Wild Oats.—False wild oats differ from the cultivated varieties in the production of heavier awns, in heavy pubescence, and in the basal articulation. False wild oats resembling cultivated varieties in color and panicle characters have been found by numerous investigators. Nilsson-Ehle (1911a) has reported false wild oats in 11 pure-line selections and in 2 commercial varieties belonging either to *A. sativa* or *A. sativa orientalis*. A heterozygous false wild form was found in the second generation of a cross between *sativa* varieties. It gave a ratio of 1 cultivated:2 heterozygous:1 false wild form. The heterozygous forms are less heavily awned than the false wild and have the *fatua* type of callus only on the lower grain. In recent years, various investigators have observed many cases of false wild oats which have occurred in cultivated varieties (Akerman, 1921; Garber, 1922b; Marquand, 1922). Studies of inheritance prove that it is very improbable that false wild oats have been obtained from natural crossing, the hypothesis presented by Zade (1918). A common reason for this conclusion is that segregation in false wild-cultivated crosses is very different from that obtained in crosses of *Avena fatua* with *A. sativa*. Garber and Quisenberry (1923) attacked the problem by studying delayed germination. Seeds of the wild oat,

A. fatua, have the property of delayed germination and this character was inherited in crosses of *fatua* with *sativa* varieties. Delayed germination was not found in homozygous or heterozygous false wild forms. Goulden (1926) and Huskins (1926) found cytological irregularities in false wild oats, abnormal pairing of chromosomes and other chromosome aberrations. Huskins believes that some chromosomal aberration, rather than a change in a single gene, is instrumental in causing the appearance of false wild oats. Considerable difference of opinion is held regarding the cause of the production of false wild oats. Whether they originate as a loss mutation or through hybridization or both is not yet determined. Some evidence for hybridization and some for mutation has been obtained.

CLASSIFICATION AND INHERITANCE IN BARLEY

Students of barley classification have frequently used density and fertility of the lateral florets as chief means of separating the larger cultivated groups. While density is quite a stable character, there are gradations in the length of the internode from the very lax to the very dense spikes without any clear-cut differentiation between the middense and midlax groups. While density is an important character by means of which to differentiate forms, it is not very usable as a chief means of species or group classification. Harlan (1918) has made an interesting review of barley-classification studies and has presented a new grouping in which species are made on the basis of fertility of the lateral florets. The following key is taken from Harlan's paper:

- All spikelets fertile (six-rowed barley)
 - Lemmas of all florets awned or hooded..... *Hordeum vulgare* L.
 - Lemmas of lateral florets without awns or hoods *H. intermedium* Kecke.
- Only the central spikelets fertile (two-rowed barley)
 - Lateral spikelets consisting of outer glumes, lemma, palea, rachilla, and usually rudiments of sexual organs *H. distichon* L.
 - Lateral spikelets reduced usually to only the outer glumes and rachilla, rarely more than one flowering glume present and never rudiments of sexual organs.... *H. deficiens* Steud.

It seems very probable that the *H. intermedium* group could be classified more accurately by considering that the lateral florets were only partially fertile instead of fully fertile.

There are several contrasting characters by means of which variety groups are made. Harlan has used the following to differentiate the variety groups belonging to each of the four species groups:

- Seeds hulled; seeds naked.
- Lemmas awned; lemmas hooded.
- Seeds white, blue, purple; seeds black.

In classifying the cultivated varieties of barleys, the density of the spike, its shape, and the appearance of the awns as well as the color of

the seed, have been used. Smooth-awned varieties are being produced and it is only a question of time before nearly all awned varieties will be represented by both the rough and smooth-awned forms.

Species Crosses.—Two general results have been obtained from crossing two- and six-rowed varieties. The most frequent result is an inter-



FIG. 34.—Individual spikes of F_2 generation of cross of Svanhals \times Manchuria representing phenotypic progeny classes in which the lemmas of the lateral florets are rounded and awnless. From left to right: The two-rowed class which will breed true in P_3 ; low fertility class which will give two-rowed, low fertility and *intermedium* in F_3 ; *intermedium*, which will breed true for *intermedium* habit in P_3 . (After Harlan and Hayes, 1920.)

mediate condition in F_1 in which the lateral florets are awned, but produce little or no fruitfulness. In F_2 a 1:2:1 ratio of six-rowed, intermediate, and two-rowed forms is obtained. Six- and two-rowed forms breed true to these respective characters in later generations. Results of this nature can easily be explained on a single main-factor difference (Biffen, 1907b; Gaines, 1917).

The *intermedium* barleys have generally been considered to be of hybrid origin. A cooperative study carried on at the Minnesota Experiment Station has shown the probable origin of some *intermedium* forms (Harlan and Hayes, 1920). In a cross between Manchuria, a six-rowed

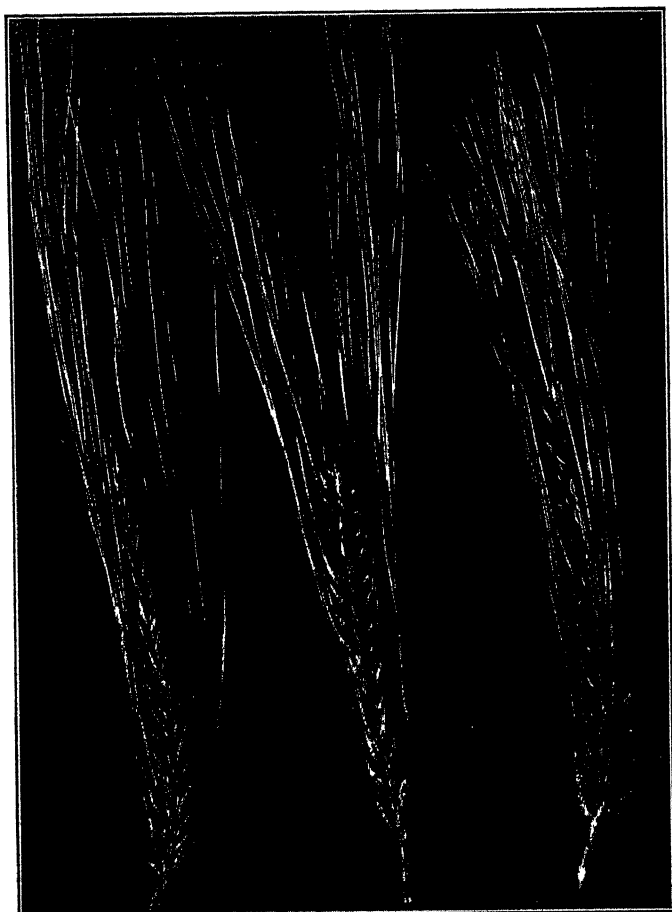


FIG. 35.—Individual spikes of F_2 generation of cross of Svanhals \times Manchuria representing the phenotypic progeny classes in which lateral florets bear awns. From left to right. Low fertility awned plant which will give all classes of segregates in F_3 as in F_2 ; high fertility awned which will segregate into *intermedium*, high fertility awned and six-rowed in F_3 ; six-rowed which will breed true in F_3 . (After Harlan and Hayes, 1920.)

barley, and Svanhals, a two-rowed variety, the F_1 was slightly fruitful and produced intermediate developed awns on the lateral florets. In F_2 a wide range of forms was obtained. The genetic nature of the F_2 plants was determined by growing seed of each in F_3 . From the F_3 results it was possible to classify F_2 plants as follows:

1. Those that bred true for the six-rowed character.
2. Those that segregated, giving six-rowed, awned, intermediate forms with very high fruitfulness of the lateral florets and *intermedium* forms in a 1: 2: 1 ratio.
3. *Intermedium* forms that bred true, giving few or no awns on lateral florets and producing approximately 50 per cent of barren lateral florets.
4. Those that gave all forms as in F_2 .
5. Those that produced intermediates and two-rowed types.
6. Those that produced six-rowed, awned intermediates with little or no fruitfulness in the lateral florets and two-rowed forms in a 1: 2: 1 ratio.
7. Those that bred true for the two-rowed condition.

Results were accurately explained by considering the Manchuria parent to contain two factors, one for six-rowed and one for *intermedium*, which was hypostatic to the six-rowed factor. It was thought possible that minor modifying factors were sometimes present which influenced the degree of fruitfulness of the lateral florets.

Crosses between *intermedium* and six-rowed forms gave intermediates of high fruitfulness in F_1 and a ratio of six-rowed to intermediates in F_2 which indicated a single factor difference. *Intermedium* forms crossed with two-rowed gave awnless forms with very low fruitfulness in F_1 and a ratio indicating one main factor difference in F_2 .

Biffen (1907b) found the *deficiens* condition dominant in a cross between *deficiens* and two-rowed. Results from an F_2 generation of a similar cross grown at the Minnesota Station indicate that it is almost impossible to separate *deficiens*, two-rowed, and intermediates by inspection. No other strains except the parental forms and various grades of intermediates were obtained.

These facts indicate that a classification made on the basis of fertility for the species groups is reliable.

The Barley Awn in Relation to Yield.—(One of the ultimate aims of the crop breeder should be to discover the physiological reason why some varieties prove superior to others. The long, rough awn of barley makes the crop very disagreeable to handle. Hooded varieties have been frequently tried out but have not been extensively grown because they do not yield as well as standard-awned strains. Likewise, many hooded hybrids have been produced but none has proved satisfactory. The facts lead to the conclusion that "the awn is an organ that is functional under most conditions, and especially in those sections where humid weather prevails, at ripening time" (Harlan & Anthony, 1920).

The fact that the awns of barley have a considerable effect on the rapidity and the amount of transpiration was determined by Zobl and Mikosch (1892). The time of greatest transpiration occurred at the time of carbohydrate formation in the seed, especially at the time of rapid starch infiltration of reserve material in the fruit. Schmid (1890, pp. 328-330) further studied and presented data on the morphology of the awn of cereals. He emphasized the fact that breeders of small grains

should give due weight to the importance of the awn. Perlitius (1903) made careful studies with awned and awnless varieties of spring and winter wheat and with barley. His studies corroborated those of Schmid, Zoebl, and Mikosch. Normal awned spikes of barley gave off nearly three times as much water as spikes with the awns removed, while with wheat the ratio was about 2:1.

Perlitius, likewise, showed that the awn has a marked effect on kernel development. Thus the ratio of size of seed at the milk stage for awned wheat, awnless wheat, and awned wheat with awns removed, was 100:88:91. With barley the differences were somewhat greater. The awned wheat likewise gave considerable increase in starch content over the awnless, and the awnless wheat showed a somewhat greater shriveling of the seed than the awned varieties.

Grantham (1919) compared awnless and awned varieties of wheat. Awnless wheats were found to be more susceptible to plant diseases, such as scab, and likewise yielded somewhat less on the average than bearded wheats. Experiments with wheat at the Minnesota Station (Hayes, 1923) proved that the awned segregates produced plumper and longer grains and yielded more on the average than the awnless. The differences in some of these experiments are independent of such factors as shattering and clearly prove that under some conditions the awn is an important physiological organ. This illustrates the importance to the plant breeder of a knowledge of the physiologic functions of certain plant organs.

The production of high-yielding, smooth-awned varieties is not a difficult task, as has been learned by cooperative studies carried on at the Minnesota Station. As smooth awn is a recessive character, all that is necessary is to cross high-yielding toothed varieties with smooth-awned sorts, and then select smooth-awned plants in F_2 . These will breed true for the smooth-awned character. Some smooth-awned segregates are not so smooth as others; these differences are genetic. Selection of the types which breed true for the fewest teeth on the awn is desirable. Numerous plants should be selected as some will prove more valuable than others for economic characters such as yield, non-shattering habit, stiffness of straw, and disease resistance.

Inheritance Studies with Barley.—There are numerous characters of barley which are easily differentiated. As the number of chromosome pairs is seven for each of the four cultivated varieties, barley furnishes ideal material for studies of linkage relations. Although the cultivated varieties have the same number of chromosomes, the *Hordeum* genus is similar to the oat and wheat genera, for the wild species of *Hordeum* are arranged in multiples of 7. Griffie obtained the following counts:

7 chromosome group: *H. spontaneum*, *H. maritimum*, *H. caput-medusae*

14 chromosome group: *H. murinum*, *H. jubatum*

21 chromosome group: *H. nodosum*

Unlike wheat and oats the economic varieties belong to the species with the lowest chromosome number. There are several barley characters which can be grouped according to their inheritance and which give simple Mendelian ratios. These are summarized in the following table:

TABLE L.—BARLEY CHARACTERS WHICH SHOW SIMPLE MENDELIAN INHERITANCE

Character differences	P_1	P_2	Authority
Hooded <i>versus</i> awned.	Hooded	3 Hooded: 1 awned	Tschermak (1901)
Rough <i>versus</i> smooth awn.	Rough	3 Rough: 1 smooth	Harlan (1920)
Black palea <i>versus</i> colorless.	Black	3 Black: 1 colorless	Tschermak (1901), Biffin (1907b)
Purple palea <i>versus</i> colorless.	Purple	3 Purple: 1 colorless	Biffin (1907b)
Hulled <i>versus</i> naked.	Hulled	3 hulled: 1 naked	Thatcher (1912) Gaines (1917)
Black pericarp <i>versus</i> white.	Black	3 Black: 1 white	Hor (1924) Kezer & Boyack (1918)

Besides these very definitely inherited character pairs, there are several other characters which make good material for studies of linkage relations.

Linkage Studies with Barley.—A study of inheritance in barley was made at the Minnesota Station in cooperation with the Office of Cereal Crops and Diseases, United States Department of Agriculture. A cross of Virginia Hooded, a six-rowed, hulled, hooded, colorless barley, with Jet, a two-rowed, naked, awned, black-glumed barley was studied. In this cross there was apparently only one factor difference between two and six rowed and the intermediate forms were classed as two rowed, although they could be differentiated from true two-rowed forms by the presence of awns on the lateral florets. The results showed that these four factor pairs were independently inherited and gave a close approximation to expectation. Crosses differing by four independently inherited, sharply differentiated factor pairs have not been frequently presented; therefore, the results are of some interest. They are as follows:

TABLE LI.—INHERITANCE OF FOUR INDEPENDENTLY INHERITED MENDELIAN CHARACTERS

	Expectation	Obtained
Hooded, two-rowed, black, hulled	129 0	113
Hooded, two-rowed, black, naked	43 0	43
Hooded, two-rowed, white, hulled	43 0	42
Hooded, six-rowed, black, hulled	43 0	56
Bearded, two-rowed, black, hulled	43 0	45
Hooded, two-rowed, white, naked	14 3	14
Hooded, six-rowed, black, naked	14 3	15
Hooded, six-rowed, white, hulled	14 3	14
Bearded, two-rowed, black, naked	14 3	14
Bearded, two-rowed, white, hulled	14 3	17
Bearded, six-rowed, black, hulled	14 3	14
Hooded, six-rowed, white, naked	4 8	4
Bearded, two-rowed, white, naked	4 8	6
Bearded, six-rowed, black, naked	4 8	6
Bearded, six rowed, white, hulled	4 8	4
Bearded, two rowed, white, naked	1 6	1
Totals	407 6	408

Apparently, these four character pairs are independently inherited. The contrasted characters are: two-rowed *versus* six rowed, black *versus* white palea, hulled *versus* naked, hooded *versus* awned. Ubisch (1916, 1919, 1921, 1923), however, found hulled *versus* naked, a factor for head density and a factor pair for long awn *versus* hooded to be linked. Hor (1924) observed a linkage between the following factor pairs: rough *versus* smooth awn, long *versus* short hairs on rachilla, and black *versus* white palea. Vavilov (1921) found a linkage between two-rowed *versus* six-rowed, rough *versus* smooth awn and hulled *versus* naked. It should be mentioned that Vavilov found several factors involved in the inheritance of rough *versus* smooth awn. Griffee (1925) obtained a linkage between early *versus* late heading and two-rowed *versus* six-rowed. These differences may be explained on the basis of differences in the genetic condition of the varieties worked with. It seems unwise to summarize these studies in greater detail at present because of the lack of agreement of the results obtained by different workers. The studies in barley linkages now being conducted will soon serve to show the reason for the differences so far obtained by different workers.

Resistance and susceptibility to attacks of *Helminthosporium sativum* P. B. and K. were found to be inherited characters and of considerable importance in relation to yield (Hayes and others, 1923). Griffee (1925) found linkage relations between reaction to this pathogene and the character pairs rough *versus* smooth, early *versus* late heading, and black *versus* white palea. This led to the conclusion that there were at least three factor pairs which condition reaction to *H. sativum*. The linkages observed were broken in later generations which indicate that they were of a genetic nature.

Nilsson-Ehle (1922) and others have reported chlorophyll deficiencies in barley. Nilsson-Ehle has reported six different types; three whites, two yellows, and one chlorina. Different whites may appear alike but are dependent upon genetic factors

located in different loci. Nilsson-Ehle found one of his whites closely linked with chlorina.

Inheritance of Other Characters.—Miyazawa (1918) and So (1918) independently found xenia when white-seeded varieties were pollinated with black-seeded strains. Engledow (1920) and Hor (1924) studied the inheritance of two forms of rachilla hairs: long, stiff, and fine, and short and slightly curled. These were called bristly and smooth, respectively, and ratios approximately of 3 bristly:1 smooth were obtained in F_2 . Nilsson-Ehle (1920) studied reaction to the nematode disease caused by *Heterodera schachtii*. Immunity was dominant to susceptibility and an approximation of a ratio of 3:1 was obtained in the segregating generations.

SOME RYE STUDIES

Wild rye, *Secale montanum*, differs from cultivated rye in its perennial habit. Tschermak (1914) finds that wild and cultivated forms may be easily crossed, which indicates rather close relationship.

Engler-Gilg (1919) believes that cultivated rye, *Secale cereale* L., originated from *S. montanum*, which grows wild in Southern Europe and adjoining regions in Asia. It is thought that rye was cultivated in the Bronze period. Vavilov (1917) doubts whether the evidence is sufficient to prove that *S. cereale* descended from *S. montanum*. He states that *S. cereale* is widely found through the southwest of Asia in barley and wheat plantings where rye has not been grown as a cultivated crop. Schultz (1919) believes cultivated rye descended from *Secale anatolicum* Boissier, which is now found growing wild in Syria, Armenia, Persia, Afghanistan, Turkestan, Sungari, and the Kirghiz Steppe.

Rye (see Chap. VI) differs from the other small grains in that it is cross-pollinated. During the last few years rye has been bred by controlled pollination. The most extensive studies have been conducted by Heribert-Nilsson (1916, 1919, 1921) who finds parchment bags, if they can be protected from wind and rain, an ideal means of insuring self-pollination. Heribert-Nilsson finds 1 or 2 plants in every 100 which appear highly self-fertile. In 1921, some strains had been inbred for nine generations. Most selfed strains were less vigorous than normal rye although a few strains were obtained which proved vigorous and yielded more than the normal variety. A variety called "Stormrag" which excels in stiffness of straw, was produced by recombining selfed strains. Brewbaker (1926) obtained similar results at Minnesota and concludes that "selection in self-fertilized lines is not only feasible but is the most effective and practical mode of rye improvement." These self-fertilized strains have aided in studies of the inheritance of characters.

Studies of Inheritance.—Rye has usually seven, sometimes eight, pairs of chromosomes (Gotoh, 1924; Belling, 1925).

Xenia in rye was first discovered by Giltay in 1893. It was later corroborated by Von Rümker and others (1913 and 1914). By continuous selection, strains have been produced which are pure for color differences.

According to Von Rümker, selection for 7 or 8 years was necessary in order to isolate strains which were homozygous for color of seed. He found the color to be located in the aleurone layer just inside the epidermis. There are numerous colors of rye which are roughly analogous to the aleurone colors of corn. The inheritance of these colors has not as yet been intensively studied. Von Rümker has isolated pure races for greenish-blue, deep brown, and yellow seed. There are also deep blue, light brown, and striped seed besides other color variations. In crosses between green- and yellow seeded strains Von Rümker found green dominant and obtained a ratio of 3 green 1 yellow in F_2 .

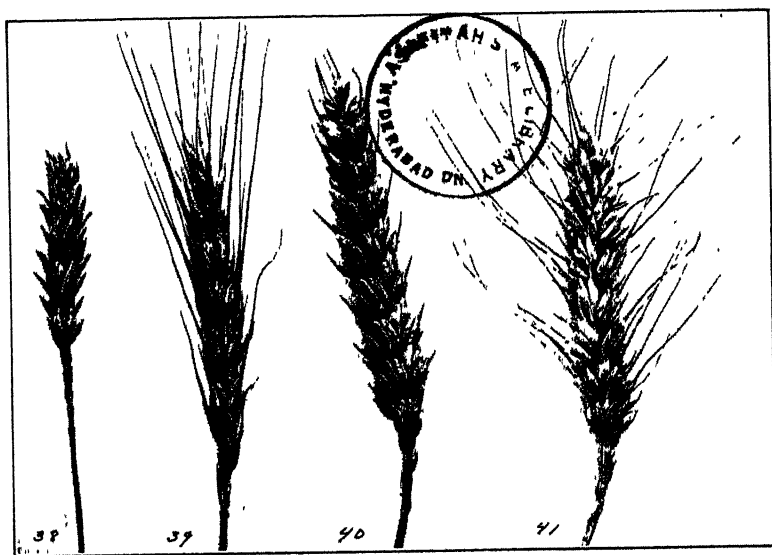


FIG. 36.—Spikes from four F_4 plants of a wheat-rye cross. Spike No 39 is much like rye in regard to the awn development and ciliated glumes. Other heads resemble wheat more than rye (After Love.)

There are both spring and winter varieties of rye. The spring habit appears to be a dominant character, for Tscherniak (1906) obtained a ratio in F_2 of 3 spring forms:1 winter form.

Brewbaker (1926) studied several different chlorophyll deficiencies and concludes that practically all are recessive to normal. Heribert-Nilsson (1919) studied a wax-free type which is also recessive. Brittle plants were studied by Brewbaker and were found to be a simple recessive. These plants can be recognized in the field because the culms break so easily. It was learned (Davidson and others, 1924) that brittle plants have a thinner cell wall, a lower, crude fiber content, a higher pentosan content, and less lignin than normal plants.

Mains and Leighty (1923) and Mains (1926) reported studies of disease resistance with rye. Strains have been obtained from Abruzzes rye which are resistant to leaf rust, *Puccinia dispersa*; stem rust, *Puccinia graminis secalis*; and mildew, *Erysiphe graminis secalis*. Resistance to each of the diseases appears to be due to a separate genetic factor or set of factors.

Wheat-rye Hybrids.—Numerous investigators (Backhouse, 1916–1917; Leighty, 1915, 1916, 1920; Jesenko, 1911, 1913; McFadden, 1917; Meister, 1921; Gaines and Stevenson, 1922) reported natural or artificial crosses between wheat and rye. Both Leighty and Meister have observed that natural crossing is more frequent in some seasons than in others. In most successful crosses, wheat has been used as the female parent, although Gaines and Stevenson (1922) reported successful rye-wheat crosses with Rosen rye as the female parent. The F_1 and F_2 generations of the rye-wheat hybrids resembled rye much more strongly than wheat while the wheat-rye hybrids are more wheatlike. Segregation in wheat-rye crosses occurs for some characters and, as winter rye is much more cold resistant than winter wheat, it is only natural to try and improve winter wheat by a rye-wheat cross. As a rule, the F_1 cross is self-sterile, although back crosses with the parents have sometimes been successful. Love and Craig (1919a) have described a successful wheat-rye cross, using Dawson's Golden Chaff as the wheat parent. Studies have been continued through F_4 and F_5 and a number of plants have been obtained which exhibit little or no sterility. These plants are wheatlike in spike and seed characters, yet they resemble rye in some other characters. They are now being tested for winter hardiness.

BUCKWHEAT

Buckwheat belongs to the buckwheat family, *Polygonaceae*. The original home of this plant was probably Asia,¹ whence it was introduced into Europe through Tartary and Russia in the Middle Ages. The generic name of buckwheat, *Fagopyrum*, comes from the Latin, *fagus*, beech, and the Greek, *puros*, wheat, based on the fact that the seed of buckwheat resembles the beechnut. The two species of economic importance are *F. tataricum*, and *F. esculentum*. The forms commonly grown in the United States belong to the last-named species. Another species, *F. emarginatum*, is sometimes designated but some plant breeders prefer to consider it as a variety of *F. esculentum*.

Classification is based on such characters as size, color, and shape of seed; color of growing stem; average height of plant; shape of leaf; and flower characters. The flowers of buckwheat are dimorphic, *i.e.*, some have long stamens and short styles, others just the reverse. In

¹ CARLETON (1916).

general, only one kind of flower is produced on the same plant. Dimorphism facilitates cross-pollination.

Species Relationship.—The two species of buckwheat differ strikingly with regard to their ability to set selfed seed under a cover. Althausen (1910a) pointed out that *F. tataricum* was spontaneously self-fertile. This has been corroborated at the West Virginia Experiment Station. The varieties Rye, Mountain, and a notch-seeded buckwheat, all belonging to the *tataricum* species, set seed abundantly under glassine bags. On the other hand selfed seed was relatively difficult to obtain from varieties of *F. esculentum*, such as Japanese Silverhull and Gray. The



FIG. 37.—Chromosome of buckwheat. At left, cell from root tip of *F. emarginatum* showing diploid number of 16; at right, pollen mother cell from *F. esculentum* with 8 haploid chromosomes. (After Quisenberry)

latter species has showy flowers that are distinctly dimorphic whereas *F. tataricum* has relatively insignificant flowers that are not distinctly dimorphic. Insects, particularly honeybees, visit the flowers of *F. esculentum* in great numbers. Stevens (1912) concludes that in this species natural self-fertilization seldom occurs owing to the relatively slow pollen tube growth in selfed flowers. With respect to chromosome number *F. esculentum* and *F. tataricum*, are apparently alike. Quisenberry (1926) found the diploid number to be 16 (see Fig. 37).

Inheritance Studies.—Most of the buckwheat inheritance studies reported have been confined to *F. esculentum*. The inheritance of length of style has been investigated by Althausen (1908), Dalgren (1922), Egiz (1925), and at the West Virginia Experiment Station. Short styles are dominant to long styles and are apparently controlled in their inheritance by a single factor difference. With respect to flower color Althausen

(1910b) found that white-flowered forms bred true, whereas red-flowered forms segregated. The inheritance of height of plant in buckwheat was explained by Egiz on the basis of a single factor difference.

Breeding Buckwheat.—It has been pointed out that, although somewhat difficult, self-fertilization of *F. esculentum* may be accomplished. No evidence of definite degeneration as a result of repeated illegitimate pollination was found by Egiz (1925). Certain races of buckwheat when self-fertilized produced well-filled grains and normal descendents. Strains of *F. tataricum* may be selfed with ease and, hence, there is no particular difficulty involved in breeding this species by controlling pollination and practicing selection.

Relatively little attention has been given to the improvement of buckwheat by breeding. There is considerable variation in type and undoubtedly strains could be isolated which would surpass present commercial varieties.

RICE

Rice is thought by Carleton (1916) to have "originated somewhere in the region of China to India inclusive." It has not been recorded with other cereals that were grown in Egypt in ancient times. Comparatively little study has been made regarding classification and genetic relationship of the wild and cultivated species.

Cultivated races are classified into glutinous and non-glutinous groups. Other characters of importance in varietal classification are size, shape, and color of seed; color of glumes and leaf sheath; awned or awnless glumes; and length of glumes, whether long or short. A short summary of inheritance of some individual characters is of interest (see Table LII).

Inheritance of Characters.—The endosperm of rice is glutinous or starchy. The glutinous group is not grown in the United States nor generally in Europe as a commercial crop. When cooked, it runs together into a pasty mass while the seeds of common rice keep their shape when properly cooked. The starch of ordinary rice is replaced by a carbohydrate of a different form. Apparently one Mendelian factor difference separates these groups. The color of the pericarp is dependent upon several factors and various ratios—3:1, 9:7, and 9:3:4—have been reported. Considerable study of the inheritance of colors in various parts of the plant have been made. One to several genetic factors are involved. A factor or group of factors often have a pleiotrophic effect. Hector (1922) concluded that this is a result of several closely linked factors. Takahasi (1923) explained certain experimental results by a linkage of a factor for character of endosperm with one of the factors which conditions red color of awns or glume tips.

TABLE LII.—SUMMARY OF THE INHERITANCE OF THE CHARACTERS OF RICE

Contrasted characters	F ₁	F ₂	Authority
Character of endosperm	Starchy	3 starchy:1 glutinous	Ikeno, 1914, Hoshino, 1915
Red <i>versus</i> white seed coat	Red	3 red. 1 white	Thompson, 1913, Ikeno, 1918;
		9 red. 7 grey, brown, and white	Parnell, <i>et al.</i> , 1917, Ikeno, 1914;
		9 red. 3 yellow. 4 white	Kato and Iwakawa, Z., 1921
Color in various plant parts	Generally colored although sometimes colorless	3:1, 9:7, 27:37, 15:1 ratios	Ikeno, 1918, Thompson, 1915;
		Frequently inherited as a group or system, closely linked factors	Parnell, <i>et al.</i> , 1917, 1922, Takezaki, 1921, 1923
Susceptibility to disease caused by <i>Leptosphaeria oryzae</i> <i>versus</i> immunity	Susceptibility		Hector, 1922
Immunity and susceptibility to American "rice blast" caused by <i>Piricularia oryzae</i>	Immunity	3 immune 1 susceptible	Ikeno, 1918
			Sasaki, 1922
QUANTITATIVE CHARACTERS			
High <i>versus</i> low stature	F ₁ almost perfectly dominant	Complex segregation (multiple factors)	Ikeno, 1918
Long <i>versus</i> short panicle			
Thick <i>versus</i> thin stem			
Amount of tillering			
Time of appearance of first panicle	F ₁ intermediate	Complex segregation (multiple factors)	Ikeno, 1918
Compact <i>versus</i> loose grain arrangement			
Broad <i>versus</i> narrow leaf			
Time of flowering	Intermediate		
Quality of grain and yield		Segregation Improvement in later years in quality and yield	Hoshino, 1915 Kock, 1917

The inheritance of plant characters may be explained by the usual Mendelian method. The ratios given show that color inheritance may be explained by one or more factors. Ikeno (1918) studied the inheritance of a number of size characters. In some cases dominance was obtained in F_1 . In other characters the F_1 was intermediate. Complex segregation occurred in F_2 but with no definite ratios. Multiple factors were used to explain the results.

Terao (1921) observed a type of semisterile plant in certain pedigreed strains of rice which had formerly produced only fertile progeny. The frequency of appearance in two families, each derived from a single parent, was 1 semisterile to 117 and 114 fertiles, respectively. Progeny of semisteriles segregate in a 1:1 ratio of normal and semisterile plants. Semisterility is explained by the hypothesis of a sex-linked lethal factor, a , which causes the death of the female gametes, but which does not affect the male gametes. Thus a semisterile plant, Aa produces only female gametes A and male gametes A and a . The original mutation of A to a was supposed to be the cause of the semisterile plants. A different type of semisterility which first appeared in a pure line has been described by Kondo and Ono (1923). The progeny bred true for semisterility. Terao (1922) described a change in the "large-grained" rice which he believes is a result of a factor mutation. Large-grained rice is characterized by panicles with a smaller number of spikelets than normal and with larger spikelets and seeds than in the normal. The larger-grained type is recessive to normal and a few normals appear in the progeny of large grained, even though the flowers are protected from cross pollination. Mosaic forms sometimes occur in large-grained plants. These mosaics are characterized by sectants of normal grains on large-grained plants. Terao supposes recessive a in large-grained plants suddenly changes to A . These Aa sectants are supposed to occur in meristematic tissue and may be so small that they may be overlooked. The progeny of such plants are largely "large-grained" although a few normals will be obtained also.

Nakatomi (1923) studied chromosome numbers in 21 races of rice consisting of anomalous types produced by mutation and normal races. Twelve is the haploid chromosome number although the sizes of chromosomes varied more or less in different races.

Time of culm formation was carefully studied by Hoshino (1915), who crossed an early with a late variety. The parents averaged 83.8 and 113.2 days, respectively, from time of planting to jointing, the parental average being 98.5 days, while the F_1 gave an average of 94 days from planting to jointing. The F_2 generation equalled the combined range of the parents. Some forms bred true to the parental types in F_3 . One form which segregated in F_3 was much less variable than the F_2 . This line could be explained by the presence of a single heterozygous factor for

time of shooting. The author suggests that three multiple factors will explain the results.

Kock (1917) crossed Karang Serang, an early maturing, good-quality rice, with Skrivinankotti, a variety of high-yielding ability. Results were not easily explained on a factor basis. After 7 years some hybrids showed considerable uniformity. Improvement in quality and quantity of yield were obtained as shown by a comparison of the parents and the better of these hybrid lines.

The pure-line method of breeding rice as well as hybridization has been of value in producing new varieties. Chambliss and Jenkins (1923) described several improved varieties produced at the Rice Experiment Station, Crowley, La. Methods of breeding rice are similar to those described for other normally self-pollinated small grains.

CHAPTER XII

COWPEAS, SOYBEANS, AND VELVET BEANS

Cowpeas, soybeans, and velvet beans belong to the group of naturally self-fertilized crops. The fundamental principles involved in breeding crops of this group have already been discussed. It suffices here to point out that the method of breeding these three legumes does not differ essentially from that for the group.

COWPEAS (*Vigna sinensis*)

Origin.—A wild plant closely related to the cultivated cowpea grows quite generally over the continent of Africa. The wild form differs from the cultivated in having smaller seeds and in having pod valves which coil in ripening. The two forms may be hybridized with ease. This fact and the fact that wild cowpeas have been found in no other place, are generally accepted as evidence (Piper, 1916) that the cultivated form arose in Africa.

Description and Inheritance.—The cowpea resembles the garden bean in general appearance. Some varieties grow erect while others are vine-like and trail over the ground. The pods are rather long and contain from 6 to 15 seeds each. Flowers are white or nearly white and pale to medium violet purple and are shaped like those of the garden pea. Seed coats vary a great deal in color—some are mottled, others unicolored. The life period of this plant is too long to permit its growth very far north, and for this reason an earlier maturing cowpea is desirable.

Size and shape of pod and seed have been used to separate the larger groups. No studies of inheritance of these major differential characters have been made.

Color inheritance with particular reference to the seed coat has been studied by Spillman (1911) and more recently by Harland (1919*a*, *b*, *c*, 1920). Anthocyanin coloration in the stem and leaf stalk is dependent on a single factor difference *X*, dominant to its absence. The inheritance of seed-coat pattern involves factors *B* (black), *N* (buff), *M* (Maroon) and *R* (Red).

Factor system for seed-coat colors:

Black	<i>B</i>	<i>N</i>	<i>M</i>	<i>R</i>
Black	<i>B</i>	<i>N</i>	<i>m</i>	<i>R</i>
Black	<i>B</i>	<i>n</i>	<i>m</i>	<i>R</i>
Black	<i>B</i>	<i>n</i>	<i>M</i>	<i>R</i>
Brown	<i>b</i>	<i>N</i>	<i>M</i>	<i>R</i>
Buff	<i>b</i>	<i>N</i>	<i>m</i>	<i>R</i>
Maroon	<i>b</i>	<i>n</i>	<i>M</i>	<i>R</i>
Red	<i>b</i>	<i>n</i>	<i>m</i>	<i>R</i>
New-Era pattern	<i>E</i>	<i>R</i>		
White				Absence of <i>R</i>

Purple color of the ripe pod is dependent on one main factor difference *P*. Each of the three factors *B*, *E*, and *P* produces anthocyanin pigmentation in the young pod, calyx, and peduncle. Whether these three factors, each dominant to its absence, constitute a triple series of multiple allelomorphs or occupy different loci very near together in the same chromosome, has not yet been established.

In crosses between black cowpeas and the variety Black Eye, Spillman found the patterns known as Holstein (pigmented area covering micropylar end and isolated spots of pigment on the non-pigmented area) and Watson Eye (pigmented area around hilum with indistinct margin at micropylar end of seed, micropylar end covered with fine dots of pigment) appearing in the F_2 generation. This indicated the origin of varieties which bear these seed-coat patterns.

The inheritance of flower color in the cowpea, according to Harland, is rather simple. In crosses between dark and pale, also between dark and white, the segregation in the F_2 generation proved to be that of a monohybrid with dark behaving as the dominant. Spillman (1913) found correlations between the production of certain seed-coat colors and the occurrence of anthocyanin in the flowers.

Root knot (*Heterodera radicicola*) and wilt (*Neocosmospora vasinfecta*, var. *tracheiphila*) are the two most serious diseases of cowpeas. The former is due to the attack of a nematode, the latter is due to a fungus. The variety known as the Iron cowpea possesses resistance to both of these diseases. According to Orton (1911) this disease resistance is inherited as a dominant character. The F_2 generation is too variable to be satisfactorily explained on a monohybrid basis. Resistance is, however, definitely inherited and can be easily isolated from the segregating generations after a cross has been made.

Some Results of Selection and Crossing.—The characteristics of an ideal cowpea are resistance to nematodes and wilt, upright habit of growth with pods borne high, and high-yielding ability. With this ideal in view the United States Department of Agriculture has conducted extensive investigations.

Attention was first called to the Iron cowpea by T. S. Williams of Monetta, S. C. He found it would thrive on "pea-sick" soil where other varieties were a complete failure. On learning of this resistant variety, Orton gave it a thorough trial and found it possessed resistance. Measures were immediately taken to increase and disseminate the Iron cowpea generally throughout the southern United States. Because the Iron variety did not produce as large yields of seed and forage as some other varieties such as Unknown, breeding was resorted to for the purpose of producing a high-yielding resistant strain (Webber and Orton, 1902; Orton, 1902).

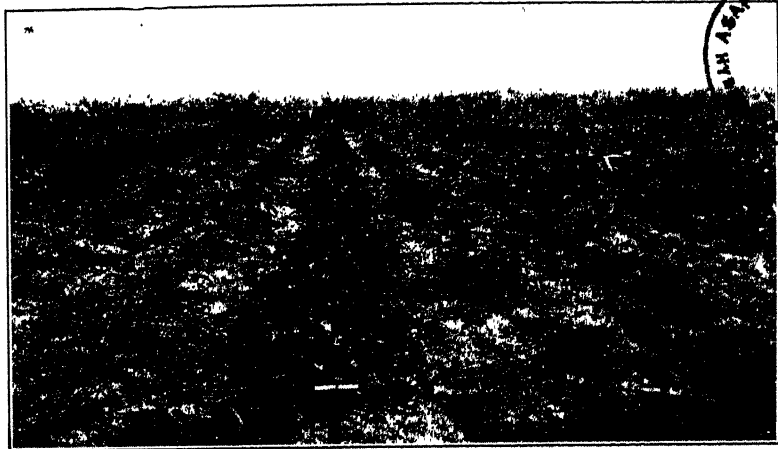


FIG. 38.—Iron cowpea vs. Black and Taylor, showing comparative resistance to the wilt and the root-knot. Iron in center and Black and Taylor at right and left respectively. (After Orton.)

In addition to disease resistance this variety has a relatively upright, bushy habit of growth but the seed production is low. At first a large number of sprawly forms, such as Red Ripper, Clay, Black, and Unknown were crossed with Iron. None of the segregates from these crosses proved particularly desirable. Later more attention was given to the selection of parents on the basis of habit of growth, fruitfulness, and position of pods. The necessity of a selection of parents on the basis of desired characters cannot be overemphasized. Whippoorwill and New Era are desirable varieties with respect to the three characters mentioned above.¹ The variety Monetta was the best segregate obtained by Orton from a cross between Whippoorwill and Iron. Brabham, a variety which has consistently shown itself superior to Monetta, is the result of the same cross made by a farmer. Both of these varieties of hybrid origin possess disease resistance and to a certain degree the other desir-

¹ The following information was furnished by the courtesy of Dr. C. V. PIPER.

able agronomic characters. More recently Morse, of the Forage Crop Investigations Office, Bureau of Plant Industry, has crossed Brabham with Groit (a hybrid of Whippoorwill and New Era). Victor, one of the segregates of this cross, will be distributed in the near future. Concerning the merits of this new variety, Piper makes the following statement:

Victor cowpea is absolutely resistant to nematodes and wilt, is a tall bushy variety, extremely fruitful, and, all in all, it seems conservative to say it is by far the best variety of cowpea ever yet developed.

SOYBEANS (*Soja max*)

Origin.—The soybean is of ancient cultivation. Japan, China, Korea, Manchuria, northern India, and the islands of Java have grown this plant for centuries both as a human food and as feed for animals. In Japan and Manchuria the cultivated soybean is erect in growth. Its nearest wild relative is a small-stemmed, trailing plant with smaller flowers, pods, and seeds. This wild form is found in Japan, Manchuria, and China. The varieties of soybeans found in India are intermediate between the two types just mentioned. According to Piper and Morse (1910) all intergrades between the wild plant and the cultivated erect form may be found, so there is little doubt that all forms belong to one species (*Soja max*).

Classification and Inheritance.—The numerous varieties of soybeans show many different combinations of characters. Varieties differ in habit of growth, some being erect, others more procumbent and several truly vining. Color and shape of seed and pods, color of flowers, color of pubescence of the pod, and time of maturity are characters which have been widely used in varietal and group classifications.

Some work has been done on the inheritance of characters in soybeans. Beans with green cotyledons may have green seed coats, while beans with yellow cotyledons may have either green or yellow seed coats.¹ H. Terao (1918) of the Imperial Agricultural Experiment Station, Tokyo, Japan, has discovered that in a cross of green cotyledons, green seed coats ♀ × yellow cotyledons, yellow seed coats ♂—the inheritance of the green seed coat apparently was matroclinal; likewise, the inheritance of the character of the cotyledons. In the reciprocal cross the character of the cotyledons again proved matroclinal in inheritance but the seed-coat character segregated as a monohybrid with green dominant. In explanation of these facts it is assumed that the two kinds of chlorophyll concerned differ in that one remains green (G) and the other turns yellow (Y). It is further assumed that the inheritance of these conditions in the cotyledons is through the cytoplasm or chromatophores and not

¹ Black and brown pigments also appear in the seed coats of certain varieties.

* These pigments are entirely independent of the green and yellow colors but they make the green and yellow colors indistinct,

through the nucleus. In the case of color of seed coat a Mendelian factor pair is involved. When *H* is present it prevents the chlorophyll (*Y*) in the seed coat from changing to yellow. When this factor is absent the small letter *h* is used.

Table LIII, taken from Terao, illustrates four possible combinations. (*G*) and (*Y*) are transmitted only through the cytoplasm of the egg cell.

TABLE LIII.—INHERITANCE OF COTYLEDON AND SEED-COAT COLOR IN SOYBEAN CROSSES

	Crossing No. 1			Crossing No. 2	
Parents.....	$(G)HH \text{ } \varnothing \times (Y)hh \text{ } \sigma$			$(G)HH \text{ } \varnothing \times (Y)HH \text{ } \sigma$	
Cotyledons.....	green	yellow		green	yellow
Seed coats.....	green	yellow		green	green
<i>F</i> ₁	$(G)Hh$			$(G)HH$	
Cotyledons.....	green			green	
Seed coats.....	green			green	
<i>F</i> ₂	$(G)HH$	$(G)Hh$	$(G)hh$	$(G)HH$	
	25 per	50 per	25 per	100 per	
	cent	cent	cent	cent	
Cotyledons.....	green	green	green	green	
Seed coats.....	green	green	green	green	
	Crossing No. 3			Crossing No. 4	
Parents.....	$(Y)hh \text{ } \varnothing \times (G)HH \text{ } \sigma$			$(Y)HH \text{ } \varnothing \times (G)HH \text{ } \sigma$	
Cotyledons.....	yellow	green		yellow	green
Seed coats.....	yellow	green		green	green
<i>F</i> ₁	$(Y)Hh$			$(Y)HH$	
Cotyledons.....	yellow			yellow	
Seed coats.....	green			green	
<i>F</i> ₂	$(Y)HH$	$(Y)Hh$	$(Y)hh$	$(Y)HH$	
	25 per	50 per	25 per	100 per	
	cent	cent	cent	cent	
Cotyledons.....	yellow	yellow	yellow	yellow	
Seed coats.....	green	green	yellow	green	

Somewhat different results were obtained by Woodworth (1921) in studies of the inheritance of seed coat and cotyledon color. Yellow cotyledons were dominant to green and there was no evidence of maternal inheritance. Green seed coat proved to be dominant to yellow. Repulsion between green seed coat and yellow cotyledon and between yellow seed coat and green cotyledon was found with about 13 per cent crossing

over. The following factorial analysis was suggested to explain the results:

Y, factor for yellow pigment and cotyledon

G, factor for green pigment in cotyledon

I, factor causing green pigment to fade out at maturity, *i*, green cotyledon in absence of *D*

D, duplicate of *I*; *d*, green cotyledon, in absence of *I*

V, factor for green seed; *v*, yellow seed coat

Tawny-colored pubescence was found to be dominant to gray and the F_2 generation indicated a monohybrid segregation. In the F_2 generation of a cross involving hilum color 9 black to 7 brown were obtained. Complete linkage was found between the factor for tawny pubescence and one of the complimentary factors for black hilum.

In a later paper Woodworth (1923) reported that dark-colored pods were dominant to light colored, and purple flowers dominant to white. In each case a 3:1 segregation was obtained

Two types of growth habit were described, a tall, luxuriant, late-maturing type and a low, compact, early maturing type. In inheritance the former was found to be dominant to the latter and the F_2 generation indicated that the two types differed genetically by a single factor pair.

Breeding.—Pure-line selections of soybeans have been made on the basis of oil content, yield (both of seed and forage), persistence of leaves, and other economic characters. Varieties like Wisconsin Black retain their leaves green until practically all the pods are ripe. Another character of considerable importance in the soybean is frost resistance. It has been found in trials at the Arlington Experimental Farm near Washington, D. C., that varieties differ appreciably in this character in both early spring and late fall. Most of the late varieties were killed. This would indicate that the hereditary difference between varieties in frost resistance is without doubt in part a matter of the degree of maturity which the plants have reached at the time of frost. Considerable artificial hybridizing has been done by Morse of the United States Department of Agriculture. While soybeans have been grown in the Orient since ancient times, their general growth in the United States and Europe is comparatively recent. As a consequence, investigation with this crop has not proceeded much beyond the stage of variety testing and strain isolation. Then, too, there are so many varieties of different habits of growth that it has been possible to find a variety adapted to almost any locality. As the real value of the soybean becomes more generally appreciated, it will undoubtedly receive more attention from the breeding standpoint.

VELVET BEAN (*Stizolobium*)

Origin.—Although little is known of the early history of the velvet bean it is thought that it is a native of India. The Florida velvet bean

(*Stizolobium deeringianum*) was introduced into Florida previous to 1875 and has never been grown much farther north because of climatic limitations. Southern Georgia, Alabama, Mississippi, and Louisiana mark the northern limits of this thrifty, vigorous growing legume. Cultivated varieties of related species of *Stizolobium* have been found in the countries surrounding the Indian Ocean. The most important of these is the Lyon bean (*S. niveum*). Hybridization between this form and the Florida velvet bean has produced many different types, some of which resemble other species of *Stizolobium*. From this fact, Piper has suggested that possibly all cultivated forms of *Stizolobium* belong to a single species.

Important Characters and Inheritance.—The Florida velvet bean is an annual of extremely vigorous growth. Its branched, vinelike stems sometimes reach a length of from 30 to 50 feet. The leaves are large and compound, bearing ovate leaflets. The flowers, which are dark purple (white in some species), are borne in long racemes. The most important parts of the plant from a feeding standpoint are the pods, together with their seeds. Mature pods carry from three to five marbled, brown and gray seeds. The pods are somewhat constricted between the seeds and are covered with a velvety pubescence. Another important agronomic character is dehiscence of pod. The Lyon, which has pods nearly free from hair, scatters its seed when ripe, the Florida velvet bean does not. Pods of different varieties also differ in the degree of susceptibility to rot when in contact with moist soil. The pods of Yokohama velvet bean, from Japan, decay very easily.

Belling,¹ of the Florida Agricultural Experiment Station, has made a study of the inheritance of some of the characters of the velvet bean. He crossed the Florida velvet bean extensively with Lyon bean and to a lesser extent with Yokohama and China velvet beans. The Florida bean has a pubescence of whitish, stiff hairs on its leaf buds and young shoots while the ripe pods are covered with brownish-black, woolly, flattened hairs mixed with a few stiff hairs. These hairs average 1 millimeter in length. The Lyon bean has a whitish, stiff pubescence on its young shoots, leaf, and calyx. The hairs on the pods form a fine down and average 0.5 millimeter in length. The F_1 was covered with irritating hairs. The hairs on the pods were about 1.5 millimeters long. These contain a gummy substance in the hollow points and readily pierce the human skin, causing an irritation lasting several minutes. In F_2 , about nine-sixteenths of the plants bore stinging pods (long, stiff hairs which pierce the skin). Some were more developed than in F_1 . Two factors are necessary for the production of stinging pods. One of these factors, *B*, is contained by the Lyon bean while *C* is contained by the Velvet bean. Color of pubescence showed segregation in F_2 , giving

¹ See BELLING (1912a, 1913, 1914a,b, 1915a,b).

13 whitish to 3 black pubescent plants. The dehiscence of pods behaved as a dominant. Most of the pods on the F_1 plants burst open when mature. In the F_2 generation segregation occurred. Long pods crossed with short pods gave approximately a 3.1 ratio in the second generation although minor factors for pod length were discovered. In the inheritance of seed color it has been suggested that three factors are concerned, each of which produces some mottling even when heterozygous and in the absence of the two other factors. Purple color appears in the Florida velvet bean on the under surface of the first pair of simple leaves, on the stems as a mark on the leaf axil, on the wings and standard and on the stems and petioles on the side exposed to the sun; while the Lyon lacks the purple color. Purple color proved dominant in F_1 and a 3:1 ratio was obtained in F_2 , only a single factor being involved. The characters, time of flowering, size of flower clusters, and size of plant gave unmistakable evidence of segregation in the second generation. Each of the crosses, Florida \times Lyon, Lyon \times Florida, and Florida \times Yokohama, produced about 50 per cent pollen sterility in the F_1 generation. Aborted ovules were found on plants showing pollen sterility. Belling satisfactorily explained the results by postulating two factors, K present in Florida and L present in Lyon and Yokohama. The presence of either K or L , but not both, gave rise to normal pollen and ovules. Combinations of KL or kl in the gametes resulted in pollen or ovule sterility.

Mutations.—Coe (1918) has attributed the origin of early maturing velvet beans to mutations. C. Chapman and R. W. Miller, both of Georgia, and H. L. Bloint of Alabama, separately discovered early maturing mutants growing in fields planted to corn and Florida velvet beans. Chapman's selection has been increased and distributed under the names "Georgia" and "Hundred-Day Speckled." This variety requires 120 to 130 days to mature. The "Alabama" variety, which matures in 170 to 180 days, or about 2 months earlier than the Florida velvet bean, was developed from an early maturing plant observed by Bloint.

The discovery of these early varieties has greatly increased the acreage of velvet beans by making it possible to grow them farther north. In 1914 less than 1,000,000 acres were grown, whereas, in 1917, over 5,000,000 acres were given to this crop.

Another mutation¹ which is of unusual interest because of the long viny habit of growth of the velvet bean, is the bush form discovered recently in the Alabama variety. The appearance of the bush type has been found in other normally twining beans such as the common bean, the Lima bean, the hyacinth bean, and the soybean. The above-mentioned bush or "bunch" velvet bean was discovered by R. Beasley on his farm near Kite, Ga. He carefully saved the seed of a single plant in 1914

¹ The following information was furnished by the courtesy of Dr. C. V. PIPER.

and from the resultant crop grown in 1915 obtained about 50 bushels. The United States Department of Agriculture is introducing this variety into various localities of the southern United States.

For some purposes the bush variety possesses distinct advantages. For instance when grown with corn it has no tendency to twine around the cornstalks and pull them down. It is also better suited for use as a hay crop. In appearance of pods and seeds, ability of pods to resist decay when on the ground, and time required to mature, the mutant is practically identical with the Alabama variety.

Breeding.—Some progress has been made in the improvement of the Florida velvet bean by hybridization and selection at the Florida Experiment Station. A bean is desired which will give a maximum yield of forage and seed of desirable quality. Plants with bristle-like pubescence or small seeds with thick hulls are undesirable. Dehiscent pods and also those which decay readily when lying on moist soil should be avoided. An earlier-maturing strain has been sought by crossing the Florida velvet bean, which requires about 200 days to mature, with Yokohama, which requires about 120 days. It is of interest to point out that from one cross between late varieties (Florida \times Lyon) a segregate was isolated that matured a month earlier than either parent. This promising strain called Osceola has found considerable favor in the South. Another segregate, a variety called Wakulla, obtained from the same cross, matures in approximately 120 days. This strain has an undesirable character in that it shatters its seed when ripe. The material available furnishes an opportunity to obtain further improvement by crossing and selections.

CHAPTER XIII

FLAX AND TOBACCO

FLAX

Flax has been reported to have been grown by the Lake Dwellers of Switzerland as early as 4000 to 2000 B.C. (Chap. I). Although the Egyptians and Hebrews used flax to make clothing in very ancient times, little is known of the origin of the present cultivated varieties.

Species Crosses.—Tammes (1911, 1915, 1916) has made some interesting genetic studies of flax species crosses. Reciprocal crosses were made between cultivated varieties of *Linum usitatissimum* and the wild species *L. perenne*, *austracum*, *narbonneense*, *grandiflorum*, and *angustifolium*. No seeds capable of germinating were obtained except in the *angustifolium* cross. This was considered a good cause for believing that *L. angustifolium* has the best right of any of the wild species to be considered the ancestral form of cultivated flax. This wild species differs from the common cultivated varieties in that the seeds and capsules are smaller, the edges of the partition walls of the capsule are hairy, and the capsules open at maturity. In general, crosses between hairy and glabrous races showed dominance of the hairy condition in F_1 and a segregation of 3 hairy:1 glabrous in F_2 . The open type of capsule was imperfectly dominant in F_1 , i.e., the capsule did not open as widely as in the open parent. Segregation occurred in F_2 . Parental types, i.e., homozygous open and homozygous closed lines, were produced in later generations. Three or four factors were necessary to explain results.

In a later study, Miss Tammes (1923) compared the mode of inheritance of eight independently segregating pairs of factors in the two species *L. usitatissimum* and *L. angustifolium*. Two of the same genes condition the development of the same character in the two species, five genes influence the character more strongly in the wild species and the identity of one gene has not been established. Four of the genes of *L. usitatissimum* are allelomorphous with four corresponding but more potent genes of the wild species. These facts are a further reason for the conclusion that *L. angustifolium* is the wild progenitor of cultivated flax.

Interrelation of Factors for Flower and Seed Colors.—Careful studies of the inheritance of flower and seed colors have been made. In the earlier papers (Tammes, 1911, 1914, 1915, 1916) the interactions of three factors were reported. *B* and *C* together were found to be necessary for the production of light-blue flower color and when present together with *A*,

which is an intensification factor, dark-blue flowers resulted. When *C* is homozygous in the presence of *B*, the veins of the petal are darker than the rest of the same petal. The veins are the same color as the rest of the petal when *C* is heterozygous in the presence of *B*. *B* and *A* give the same result when heterozygous as when homozygous. As an example of the care with which details were worked out and to illustrate the pleiotrophic effect of a single factor in its influence on more than one character the results presented in Table LIV are given. In this analysis *C* alone or with *A* was considered to be responsible for the production of wrinkled petals although when *B* was present it inhibited the action of *C*. *B* alone or in the presence of *A* and *C* conditioned the production of blue anthers and brown seeds. When *B* is absent the seeds and anthers are yellow.

Further studies of Miss Tammes (1922) have led to the conclusion that several other factors condition color, shape, and breadth of petal and the color of the anther and seed coat. Six factors influence petal color. These are *A*, *B*,¹ *C*,¹ *D*, *E*, and *F*. *B*¹ and *C*¹ are retained in place of *B* and *C* and are necessary for the production of color, although when *A*, *D*, *E*, and *F* are recessive extremely light-pink color is produced. *E* is an intensification factor of greater strength than *A*. When both *A* and *E* are present they have a cumulative effect. *D* with *B*¹ and *C*¹ conditioned the development of lilac color while these factors in the presence of *F* were necessary for the development of blue color.

Common blue flax, therefore, contained all six factors; light blue carried the dominant condition for all except *A* which is recessive. The recessive of *C*¹ is the usual cause of lack of color in common white flax. Blue color in the anthers is dependent upon the interaction of *B*¹, *D*, and *H*, and if any of the three are recessive, yellow anthers are produced. Thus either blue or white flowers may have either blue or yellow anthers. Color of seed coat is dependent upon a complex of factors designated by *G*. *D* inhibits the action of *G* and when both *D* and *G* are present the seed is greyish green. Furthermore, the inhibitory action of *D* is neutralized by *B*¹. *C* and *D* together produce crimpiness of the petal although *B*¹ neutralizes their action.

Miss Tammes has obtained 46 different flower colors—blue, light blue, and lilac—which illustrates the complexity of the inheritance of color. Three series of multiple alllomorphs are known. As there are 15 pairs of chromosomes in flax, the material is not very favorable for genetic linkage studies.

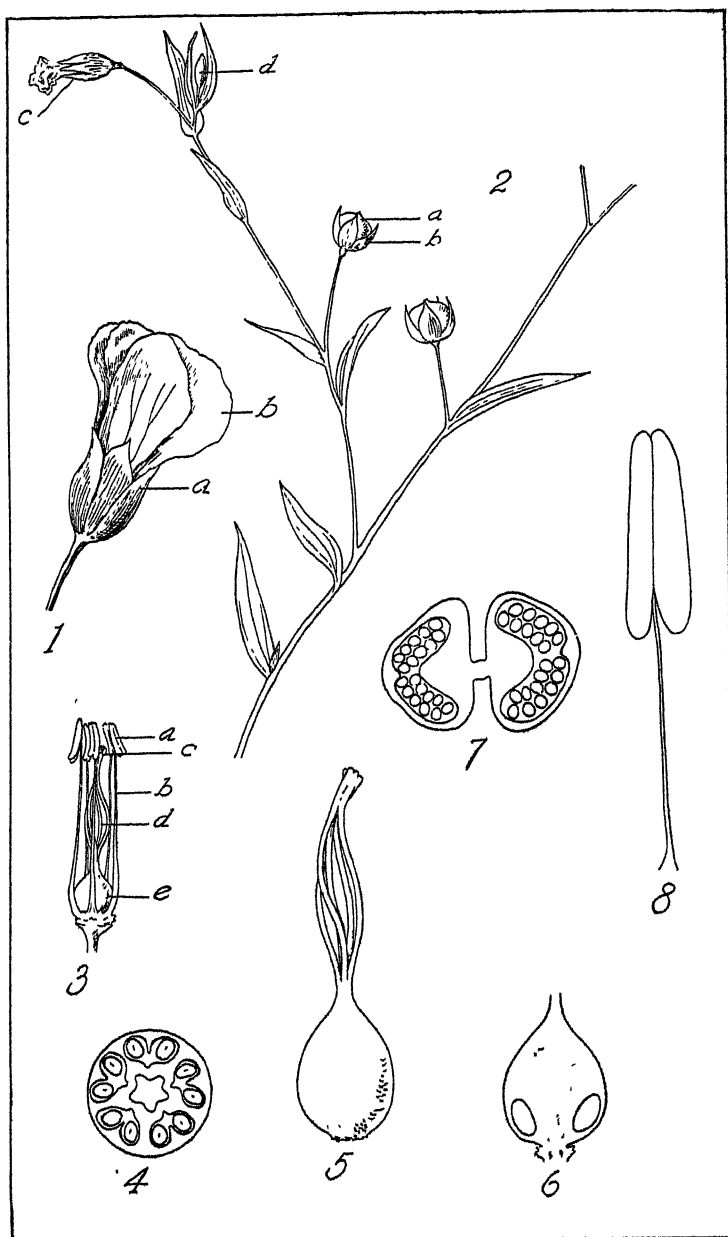


FIG. 39 — Structure of flowers of flax.

TABLE LIV.—SECOND AND THIRD GENERATORS OF A CROSS BETWEEN A WHITE FLOWERED VARIETY WITH BLUE ANTHERS AND BROWN SEED (AABB) AND A CRINKLED WHITE VARIETY WITH YELLOW ANTHERS AND YELLOW SEED (AACC)

In this table

- d.bl.flr. = dark blue flower
 l.bl.flr. = light blue flower
 w. = white flower
 c.w. = crinkled white flower
 br.s. = brown seed
 y.s. = yellow seed
 bl.st. = blue stamens
 y.st. = yellow stamens
 with v. = with darker veins than the remainder of the petal
 without v. = with veins of the same color as the body of the petal

P_2 expected	P_2 obtained	P_2 expected	P_2 obtained
1 AABBCc d.bl.flr. with v., bl.st., br.s.	3	Only d.bl.flr. with v., bl.st., br.s.	409 plants in several fami- lies.
2 AABbCC as above		d.bl.flr. with v., bl.st., br.s. 3 c.w., y.st., y.s. 1	60 21
2 AABBCc d.bl.flr. without v., bl.st., br.s.	6	d.bl.flr. with v., bl.st., br.s. 1	4
4 AABbCc as above		d.bl.flr. without v., bl.st., br.s. 2 w.flr., bl.st., br.s. 1 d.bl.flr. with v., bl.st., br.s. 3 d.bl.flr. without v., bl.st., br.s. 6 w.flr., bl.st., br.s. 3 c.w.flr., y.st., y.s. 3 w.flr., y.st., y.s. 1	8 2 31 63 34 23 9
1 AABbcc w.flr., bl.st., br.s.	3	to breed true.	1,317 plants in several fami- lies.
2 AABbcc as above		w.flr., bl.st., br.s. 3 w.flr., y.st., y.s. 1	1,271 361
1 AAbbCC c.w.flr., y.st., y.s.	3	to breed true.	395
2 AAbbCc c.w.flr., y.st., y.s.		c.w.flr., y.st., y.s. 3 w.flr., y.st., y.s. 1	obtained such segregation.
1 AAbbcc w.flr., y.st., y.s.	1	to breed true.	402

DESCRIPTION OF FIG. 39.

- Single flower—*a*, calyx; *b*, corolla.
 - Branch showing—*a*, seed; *b*, calyx; *c*, flower just after blooming; *d*, bud.
 - Calyx and corolla removed to show sexual organs in position—*a*, anther; *b*, filament; *c*, stigma; *d*, one of 5 divisions of style; *e*, ovary.
 6. Cross and longitudinal section of ovary.
 - Ovary, stigma, and 5-lobed style.
 - Cross section of anther.
 - Anther.
- Size: 1, about 5*n*; 2, about *n*; 3, nearly 4*n*; 4-8, greatly enlarged.

Inheritance of Size Characters.—Studies of length of seed were made with crosses of the wild *angustifolium* and cultivated varieties (Tammes) as well as with crosses between cultivated varieties. Seeds were of intermediate size in F_1 and segregation occurred in F_2 . The number of individuals grown was not large and the parental forms were not always again obtained. From two to four multiple factors are necessary to explain results.

Length and breadth of petal were also studied. Three forms were used, a small-petaled, white-flowered variety with a petal breadth of 3.3 millimeters, the common varieties with a breadth of 7 millimeters and an Egyptian, cultivated, blue-flowered variety with a mean breadth of petal of 13.4 millimeters. In the cross between Egyptian blue and common white the factors for color of flower and seed and for size of seed were apparently inherited independently. Breadth of petal ranged from one parent to the other in F_2 . Several factors for size of flower were necessary to explain results. The common blue with a petal breadth of 7 millimeters was crossed with the small-petaled white with an average breadth of 3.3 millimeters. In F_2 all blue-flowered segregates agreed in size with the blue parent and all white-flowered segregates had small-sized petals. The cross between Egyptian blue and the small-petaled white gave blue-flowered races with petals of intermediate size in F_1 and segregation for flower color in F_2 . The blue-flowered segregates gave a larger average breadth of petal than the white segregates. Three hundred plants of each color were examined.

TABLE LV.—CORRELATION BETWEEN COLOR OF COROLLA AND BREADTH OF PETAL IN THE F_2 GENERATIONS OF FLAX CROSSES

	Range, millimeters	Average, millimeters
300 blue-flowered plants	5 7-16 2	10 8
300 white-flowered plants	2 1-10 4	4 6
Parent Egyptian blue	10 5-16 2	13 4
Parent white flowered	2 1 4 2	3.3

These results were explained by supposing that the small-petaled white flax and the common varieties have the same factors for breadth of petal. *C*, one of the color factors, when alone or in the presence of *A* is an inhibition factor for flower size. *B*, when present, prevents the action of *C*.

Wilt Resistance in Flax.—When flax is grown for several years on the same soil, a heavy infection of *Fusarium lini* often results, and complete crop failure may occur. Bolley, as early as 1901, pointed out the true

nature of the disease and devised methods for its control. Seed treatment and crop rotation were shown to be beneficial as aids in the control of wilt. Seed selection, however, proved the most efficient control measure. In general, Bolley (1903, 1909) found that 2 or 3 years' selection under disease conditions was necessary in order to isolate a resistant variety. Both individual- and mass-selection methods were used. Similar studies carried on at the Minnesota Station (Stakman, *et al.*, 1919) have confirmed Bolley's results.

Bolley (1912) stated that no adequate explanation had been found for the accumulation of resistance when the crop was grown generation



FIG. 40.—Selected and non-selected flax on wilt-sick soil. Right foreground, non-selected flax killed by wilt; left foreground, selected flax; left background, non-selected; right background, selected. University Farm, St. Paul, Minn., 1918. (After Stakman, *et al.*, 1919.)

after generation in diseased soil. He also believed that resistant varieties would gradually lose their resistance when grown on wilt-free soil. Barker (1923) made a careful study of these questions. He found that some flax varieties contained no resistant or partially resistant genotypes. Resistance was not developed in such varieties as a result of constant association with the pathogene. Wilt-resistant pure lines did not lose their resistance when grown on clean soil. Some varieties which were wilt resistant were also resistant to flax rust caused by *Melampsoro lini*.

As an aid to seed selection in avoiding wilt, early planting is advocated. When planted early, a susceptible variety will often partially escape the serious effects of wilt. Likewise, a resistant variety frequently appears

entirely wilt free when planted early, while a later planting may show partial infection.

Tisdale (1916, 1917) has made important contributions to the nature and inheritance of wilt resistance. A high temperature proved to be an especially favorable agent in overcoming resistance. The fungus penetrates the flax plant through the stomata of seedlings, the root hairs, or the young epidermal cells. In the resistant plant, the fungus on entering stimulates cork-wall formation of cells adjacent to those attacked, which prevents further invasion. Infection of resistant plants by artificial inoculation of greenhouse or field cultures of *Fusarium lvm* did not occur in 43 trials. Check infections of susceptible plants gave 22 successful inoculations out of 47 trials. Tube cultures gave considerable infection of resistant plants although the resistance was marked when these were compared with tube cultures of susceptible strains.

The inheritance of wilt resistance was studied. A great difference in the individuality of plants of the same strain with respect to resistance was shown by their offspring. Wide variation in appearance of F_1 progeny from different crosses of susceptible and resistant plants of the same strains was obtained. Segregation occurred in F_2 . A part of the lack of uniformity of results may be explained by varying environmental conditions. Tisdale believes inheritance results can be explained by multiple factors.

Methods of Breeding.—The flax plant is grown for either seed or fiber. Varieties range in height from approximately $1\frac{1}{2}$ to more than 3 feet. Aside from differences in inheritance, the thickness of planting strongly influences the habit of growth. The fiber crop is largely produced in the Old World, while Argentina and the United States are among the leaders in seed production. Methods of breeding for seed or fiber flax are essentially the same as with the small grains.

TOBACCO

The Genus *Nicotiana*.—The tobacco genus, *Nicotiana*, has been divided by earlier workers into four sections: *Tabacum*, *Rustica*, *Petunioides*, and *Polidiella* (Don, 1838). More recently the latter two sections have been combined (East, 1912a; Setchell, 1912). East's conclusions were reached by crossing *N. bigelovii*, of the *Petunioides* section, with *N. quadrivalvis*, which was formerly placed in *Polidiella* section. *N. quadrivalvis* produces four-celled capsules and is a smaller plant than *N. bigelovii*. As the F_1 hybrid was entirely fertile, there seems no good reason for placing these forms in different sections. The four-celled capsule proved to be a partially dominant character.

From the standpoint of the student of plant genetics the *Nicotiana* genus is especially favorable material. Some of the reasons are:

1. Tobacco may be self-fertilized artificially with ease and the technic of crossing is very simple.

2. Each plant produces a large number of seeds and the seed is viable for many years.

3. There are a large number of varieties which are entirely fertile *inter se*. These furnish especially favorable material for a study of quantitative characters.

4. The different species furnish very favorable material for a study of sterility. Different crosses furnish F_1 generations which differ from each other in sterility. The range extends from species crosses which give no viable seed and from completely sterile F_1 crosses, to entirely fertile ones.

Studies of chromosome numbers with various tobacco species have been made. Goodspeed (1924) reported 9 pairs in *N. langsdorffii*, *N. alata*, and *N. longiflora*; (it is of interest that *alata* and *langsdorffii* have been used extensively by East in studies of self-sterility); 12 pairs in *N. glauca*, *N. sylvestris*, *N. paniculata*, *N. glutinosa*, and *N. acuminata*; 24 pairs in *N. tabacum*, *N. rustica*, *N. bigelovii*, and *N. nudicaulis*. Tobacco is favorable material for studies of chromosomal behavior in species crosses and for studies of chromosomal aberrations. Clausen and Goodspeed (1924) have studied a trisomic character "enlarged" which appeared in crosses of *tabacum* varieties. It was found to be dependent upon an extra chromosome. Only about 35.5 per cent of the functional ovules of "enlarged" transmit the character and about 3.4 per cent of the pollen grains. There was no evidence to support the belief that permanent increase of chromosome numbers may result from non-disjunction.

In a study of species crosses between *glutinosa* and *tabacum* which contain 12 and 24 pairs of chromosomes, respectively, Clausen and Goodspeed (1925) verified a hypothesis presented by Winge (1917). It was pointed out by Winge that successive doubling of the chromosomes would give rise to geometrical rather than arithmetical ratios. He suggested that interspecific crosses followed by doubling of chromosome numbers would better explain some results. Thus certain tetraploids would have the formula $2(n_1 + n_2)$ chromosomes, where n_1 and n_2 represent the haploid numbers. Such a condition has already been mentioned for a species cross of wheat reported by Tschermak and Bleier (1926). Clausen and Goodspeed (1925) reported a case of a cross of *N. glutinosa* \times *N. tabacum* which bred true for the F_1 appearance and which contained 72 chromosomes of the formula $2(12 + 24)$.

In another species cross (Clausen and Mann, 1924) between *N. tabacum* and *N. sylvestris*, two haploid plants were obtained. Each resembled its *tabacum* parent in all characters although on a reduced scale.

The *Tabacum* section is represented by numerous varieties of the species *Nicotiana tabacum*. These are natives of the New World. All commercial tobacco grown in the United States belongs to this species.

The Rustica section includes all the yellow-flowering species and varieties. These are of commercial importance in some countries. In India for example, they are successfully grown commercially and for some purposes prove more desirable than the *tabacum* varieties (Howard, *et al.*, 1910b, c). Among these rustica forms are three groups, (a) one in which the pistil is longer than the stamen and, therefore, one which must be artificially pollinated by hand or crossed by the aid of insects, (b) an intermediate type; and (c) forms in which the stamens and pistil are so arranged that self-fertilization is the usual rule.

The Petunioides section contains numerous varieties and species. Many of these are grown as ornamental flowering types.

Parthenogenesis.—Parthenogenesis, meaning the production of viable seed without pollination, was shown by Goodspeed (1915) to occur in *N. tabacum*, variety Cuba. Under normal conditions its occurrence is rare. Wellington (1913) did not find parthenogenesis in a considerable series of experiments and with numerous treatments under greenhouse conditions. Several species as well as several commercial varieties of *N. tabacum* were used in this study. Howard (1913) states that parthenogenesis in *N. tabacum* does not occur under normal but may occur under abnormal field conditions, at Pusa, India. The occurrence of parthenocarpy and parthenogenesis have never been observed by Howard (1924) in any of the Indian types of *Nicotiana rustica*. Howard and Ram (1924) extensively studied two varieties of *N. tabacum* furnished by Mrs. R. Haig Thomas who reported considerable parthenogenesis among varieties and hybrids of *N. tabacum* in England. No parthenogenesis was observed in India.

Sterility.—Studies of crosses between *N. tabacum* varieties and *N. sylvestris*, which belongs to the Petunioides section, have been made by Goodspeed and Clausen (1917). The F_1 generation proved to be nearly sterile, although a few apparently normal pollen grains were produced. These could not be caused to germinate in their own stigmatic fluid or in other media. A few normally maturing ovules capable of fertilization were produced by the F_1 plants. If the plants were kept under poor cultural conditions and the flowers pollinated by their respective parents, approximately 1 per cent of the number of seeds normally produced was obtained. If backcrossed with the *sylvestris* parent, practically 10 per cent of the offspring of the seeds produced are pure *sylvestris*. When crossed with *tabacum*, part of the plants from the seeds produced seem to be of normal tobacco type and are fertile; others resemble *tabacum* but are sterile. The F_1 plants closely resemble the particular variety of *N. tabacum* which is used as one of the parents.

Studies of self-sterility in tobacco crosses have been made by East (1919a, b, c). East and Park (1917, 1918) studied crosses between *N. forgetiana* and *N. alata* which are self-sterile, and *N. langsdorffii*, a self-

fertile species. *Alata* and *forgetiana* varieties sometimes produce seed late in the flowering season, although during periods of rapid growth they are entirely self-sterile. The few seeds obtained under reduced cultural conditions from selfing these self-sterile species are spoken of as cases of pseudo-fertility.

Results of crosses between self-sterile and self-fertile varieties are given in the following table:

TABLE LVI.—INHERITANCE OF STERILITY IN CROSSES BETWEEN SELF-FERTILE AND SELF-STERILE TOBACCO SPECIES

Parents	F_1	F_2	
Forgetiana \times Langsdorffii.....	Self-fertile vigorous	144 self- fertile	37 self- sterile
Alata \times Langsdorffii.....	Self-fertile vigorous	162 self- fertile	38 self- sterile

The self-fertile condition proved dominant in F_1 and a ratio of approximately 4 self-fertile:1 self-sterile plant was obtained in F_2 . The self-sterile plants of F_2 proved self-sterile in later generations. East explained these results by a dominant factor, F , for fertility and a subsidiary factor, D , for pseudo-fertility which exhibits itself only in the presence of the factors for sterility, f . This pseudo-fertility factor produces some fertility under certain conditions, thus tending to lower the number of self-sterile forms.

East has suggested that differences in the rate of pollen germination are largely responsible for the differences in the length of pollen tubes from compatible and incompatible pollinations. When self-sterile plants are self-pollinated the pollen grains germinate but the pollen tubes grow so slowly that abscission of the flower occurs before the pollen tube reaches the ovary.

East and Mangelsdorf (1925) have summarized the results of extensive studies of inheritance of self-sterility in *N. alata* and *N. forgetiana*. The following quotation is from Mangelsdorf's statement in *Botanical Abstracts*:

The progeny of a cross between two self-sterile individuals consists of a small number of sterility classes, each member of a given class being reciprocally sterile with every other member of that class; but reciprocally fertile with members of other classes. Three such classes were present in the populations studied. When members of two different classes were crossed, the progeny consisted of two of the three classes in equal numbers, the class of the female parent being always absent in the progeny.

The results were explained by the hypothesis of three allelomorphous sterility factors, S_1 , S_2 , and S_3 . The three classes were of the genotypes

S_1S_2 , S_1S_3 , and S_2S_3 . It was supposed that a plant could be fertilized only with pollen-bearing factors other than its own.

Color Characters.—Color of corolla has been studied for *Nicotiana* crosses. East (1916b) found that in crosses between *N. langsdorffii* and *N. alata* there was a dominance in F_1 of yellow over white in the color of the corolla. The *langsdorffii* parent produces blue pollen and the *alata* yellow. Reciprocal crosses gave blue pollen in F_1 , although the color was somewhat lighter than in the blue-pollen parent. Results in F_2 showed 342 plants with blue pollen and 100 plants with yellow pollen. Yellow-pollen plants bred true in F_3 . In this case a cross between species which exhibits a monohybrid ratio exists.

According to Allard (1919a) *N. tabacum* exhibits three distinct flower colors—carmine, pink, and white. In crosses between carmine and pink the F_1 was carmine. The F_1 pollinated with the carmine parent gave all carmine-colored progeny while the F_1 crossed with the pink gave carmine and pink in a ratio of 1:1. This indicates that carmine and pink differ in one genetic factor. In a cross of carmine and white the F_1 was all light carmine. In F_2 there were 54 carmine, 95 light carmine, 26 dark pink, 38 light pink, and 65 white. Some of the extracted whites revealed a tinge of color. Crosses of extracted whites with pink gave 32 carmine and 62 pink, showing that extracted whites sometimes carried a carmine factor. The factor relations are not entirely clear.

Several analyses of the inheritance of flower color have been made and several factors have been used to explain the results. Thus Clausen and Goodspeed (1921) explain various colors of the flowers of *N. tabacum* by the interaction of three factors while Sachs-Skalinska (1921) found eight independent genetic factors concerned in the complete pigmentation of *N. sundarae*.

Quantitative Characters.—Many of the so-called size characters of tobacco are of great commercial importance. For this reason their mode of inheritance is of much interest to the breeder. Extensive studies of inheritance of these size characters have been made. Inheritance of leaf number will be given as an example of a common type of inheritance of size characters in this group. Sumatra, which averages 27 leaves, was crossed with Broadleaf, which gives an average of 19.4 leaves. The results for the parents and F_1 to F_3 generations as obtained at the Connecticut Station are given in the following table (Hayes, East, and Beinhart, 1913):

TABLE LVII.—INHERITANCE OF LEAF NUMBER IN CROSS (403 × 401) SUMATRA × BROADLEAF

Number	Year grown	Generation	Leaves of parent	Range of variation	Total	Mean	C. V.
403 Sumatra..	1910	P_1	..	24-31	150	28.2 ± 0.08	5.27 ± 0.21
403-1	1911	P_2	29	23-31	125	26.5 ± 0.11	6.64 ± 0.28
403-1-2.....	1912	P_3	29	21-32	151	26.2 ± 0.12	8.28 ± 0.32
401 Broadleaf..	1910	P_1	..	17-22	150	19.2 ± 0.05	5.00 ± 0.19
401-1.....	1911	P_2	20	16-22	108	19.1 ± 0.08	6.54 ± 0.30
401-1-1.....	1912	P_3	22	17-23	145	19.9 ± 0.07	6.03 ± 0.24
403 × 401 = B.	1910	P_1	..	19-26	150	23.6 ± 0.07	5.51 ± 0.21
B-1.....	1911	P_2	25	17-32	2,402	22.7 ± 0.03	8.99 ± 0.11
B-3.....	1911	P_2	21	17-35	1,632	22.5 ± 0.03	9.51 ± 0.10
B-1-4.....	1912	P_3	25	16-29	179	22.5 ± 0.12	10.84 ± 0.39
B-1-7.....	1912	P_3	22	17-28	207	21.5 ± 0.10	10.14 ± 0.34
B-1-8.....	1912	P_3	28	19-33	82	26.3 ± 0.20	10.38 ± 0.55
B-1-10.....	1912	P_3	26	19-27	151	23.1 ± 0.10	7.75 ± 0.30
B-1-12.....	1912	P_3	25	18-30	209	23.7 ± 0.14	10.51 ± 0.41
B-1-14.....	1912	P_3	25	19-29	56	21.8 ± 0.14	7.18 ± 0.46
B-3-5.....	1912	P_3	27	17-28	159	21.7 ± 0.11	9.45 ± 0.33
B-3-6.....	1912	P_3	28	16-27	229	22.5 ± 0.09	8.71 ± 0.27
B-3-8.....	1912	P_3	25	17-23	85	20.6 ± 0.12	8.25 ± 0.43

The Broadleaf variety is commonly grown in one section of the Connecticut Valley and is especially valuable for cigar wrappers. Sumatra, which is an imported variety, produces many leaves per plant but they are small. As may be seen from an examination of the table, the F_1 had an intermediate number of leaves. Segregation occurred in F_2 and selected F_2 plants gave F_3 families which differed in the average number of leaves. B-1-14, showed the lowest coefficient of variability of any F_3 family. Progeny of this same F_2 plant were also grown at another locality and they proved uniform in number of leaves, the calculated coefficient of variability being 6.44 ± 0.27 . B-1-10 gave a low coefficient of variability and a mean leaf number which was about the same as in the F_1 generation, i.e., intermediate between the parents.

A cross was studied between Connecticut Havana, which is grown as a wrapper and binder tobacco both in the Connecticut Valley and in Wisconsin, and Cuban, a variety commonly grown under shade. The parents and F_1 gave about the same number of leaves but in F_2 transgressive segregation occurred, forms being obtained with a higher and lower leaf number than in either parent. The inheritance of size and shape of leaf was likewise investigated. The Cuban variety gives a short broad

leaf and the Havana a longer leaf which is proportionally narrower than the Cuban. Lines were obtained in F_3 which bred true, respectively, to the parental-leaf shapes.

East (1916a) has listed eight requirements, most of them independent mathematically, which should be met if size inheritance is typically

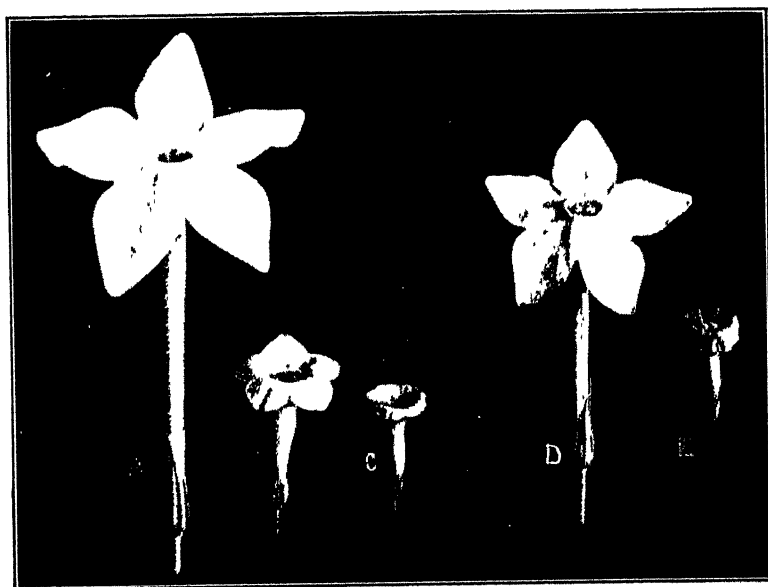


FIG 41—A, *N. alata grandiflora*; B, F_1 of *N. langsdorffii* \times *N. alata grandiflora*; C, *N. langsdorffii* (1911), D and E, extremes of the F_2 generation (1912) \times $\frac{3}{8}$. (After East.)

Mendelian, when all populations succeeding the original cross are obtained by growing progeny of single self-fertilized plants. These are:

1. Crosses between individuals belonging to races which from long continued self-fertilization or other close inbreeding approach a homozygous condition, should give F_1 populations comparable to the parental races in uniformity.

2. In all cases where the parental individuals may reasonably be presumed to approach complete homozygosity, F_2 frequency distributions arising from extreme variants of the F_1 population should be practically identical, since in this case all F_1 variation should be due to external conditions.

3. The variability of the F_2 population from such crosses should be much greater than that of the F_1 population.

4. When a sufficient number of F_2 individuals are available, the grandparental types should be recovered.

5. In certain cases individuals should be produced in F_2 that show a more extreme deviation than is found in the frequency distribution of either grandparent.

6. Individuals from various points on the frequency curve of an F_2 population should give F_3 populations differing markedly in their modes and means.

7. Individuals either from the same or from different points on the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parents to that of the F_2 generation.

8. In generations succeeding the F_2 , the variability of any family may be less but never greater than the variability of the population from which it came.

All of the above eight conditions have been obtained in experiments and no fact directly opposed to them has been discovered.

The quantitative characters in tobacco which have been studied are, therefore, typically Mendelian in their inheritance. A list of these characters and of the authority for the inheritance is here given. Not all papers on this subject are included. Those given show the general behavior of many of the characters in inheritance.

TABLE LVIII.—INHERITANCE OF TOBACCO CHARACTERS AS SHOWN BY RESULTS OF CROSSES

Character	Grown in	Authority
Height of plant.....	P_1	Jensen, 1907
Height of plant.....	P_1, F_2	Hayes, 1912
Height of plant.....	P_1 to F_4	Howard, 1913
Number of leaves.....	P_1 to F_3	Hayes, East, and Beinhart, 1913; Howard, 1913
Leaf size.....	P_1 to F_3	Hayes, East, and Beinhart, 1913; Howard, 1913
Leaf shape.....	P_1 to F_3	Howard, 1913; Hayes, East, and Beinhart, 1913
Spread, length and diameter of corolla.	P_1 to F_3	Goodspeed, 1912, 1913; East, 1916b
Sucker inheritance.....	P_1 to F_3	Johnson, 1919
Base of leaf.....	P_1 to F_3	Howard, 1913
Many characters of <i>N. rustica</i>	P_1 and F_2	Howard, 1924

The results obtained in these studies of tobacco show that segregation occurs in F_2 for size characters and that forms similar to the parents as well as new sorts may be obtained in later generations.

In some cases certain characters of commercial varieties can be explained on the basis of definite genetic factors. Kajanus (1924) found that green color of leaf was dominant over the yellow-leaf characters of White Burley and that a ratio in F_2 of approximately 15 green:1 yellow was obtained while Kelaney (1924) explained certain leaf-base characters on a definite-factor hypothesis. One of the factors for the leaf-base character was linked with a factor for flower color and gave a crossing-over percentage of 7.5.

Disease Resistance in Tobacco.—There are numerous plant diseases which are very injurious. Few studies of the mode of inheritance of

resistance and susceptibility have been made but resistant species, varieties, and strains have been observed in respect to several diseases. Anderson (1925) tested the reaction of 20 species of *Nicotiana* to wildfire caused by *Bacterium tabacum*. All 41 varieties of *N. tabacum* which were studied proved somewhat susceptible although several varieties were somewhat less susceptible than others. Several species proved resistant and all varieties of *N. rustica* proved resistant.

Valleau and Kinney (1922) reported strains of White Burley resistant to root rot caused by *Thielavia basicola*. Certain strains which are resistant to root rot are of the same type and quality as the original variety from which they were selected. Over 75,000 acres of these resistant strains were grown commercially in 1924 (Valleau, 1925). These instances lead to the conclusion that breeding disease-resistant varieties will in some cases prove a valuable means of controlling certain tobacco diseases.

Environment as a Factor in Tobacco Breeding.—It is a matter of common knowledge that environmental conditions widely modify the expression of characters. This is particularly noticeable in tobacco, where quality, size, and shape of leaf are of such marked importance. A belief has been frequently expressed that environment causes a breaking of type. The following quotation from Shamel (1910) emphasized this view for tobacco:

The writer believes that the two efficient means of inducing variability as a source of new types are change of environment and crossing. So far as the writer is concerned, the change of environment—usually the growing of southern grown seed in the north— is the most effective means of inducing variability.

Statements of this nature have been used as evidence that environment modifies the characters of a pure line by inducing variability. A careful survey of experimental studies does not support this contention. The development of the shade-grown tobacco industry in the Connecticut Valley is of interest in this discussion. This shade method first originated in Florida in 1896 and was tried experimentally in Connecticut through cooperation of the Connecticut Experiment Station and officials of the Bureau of Soils. In 1900 $\frac{1}{3}$ acre was grown and the crop sold at an average price of 72 cents per pound. A considerable acreage was grown in 1901 and the crop sold at public auction at a much higher price per pound. Indiscriminate introduction of unselected seed from Florida was practiced and in 1902 over 700 acres were grown under shade in Connecticut. The result was a disastrous failure, owing to a lack of knowledge of methods of handling and to the use of unselected seed. By further study of handling and through careful selection in which artificially self-pollinated seed was saved, the industry was placed on a firm

foundation. This latter work was carried on by the Bureau of Plant Industry (Stewart, 1908). A knowledge of Cuban methods shows that imported Cuban seed is a mixture of many types. Some experiments have shown that the breaking up alluded to is an expression of the different hereditary qualities of the parental seed plants. In 1912 Hasselbring grew a number of pure lines of tobacco in Michigan which he had formerly grown in Cuba. No evidence of breaking up of type was observed and whatever changes occurred in a pure line, owing to the new conditions, were uniformly exhibited in all plants of the pure line. Similar conclusions were reached from the immediate introduction of individual seed capsules of different tobacco plants from Cuba and their subsequent growth under shade in Connecticut (Hayes, 1914). Careful studies at Pusa, India, convinced the Howards (1910a) that new conditions did not cause a breaking up of type. They ascribed the apparent variability of new introductions to cross-fertilization, which was shown to occur frequently in tobacco.

Although there have been some differences of opinion as to the cause of variability of new introductions, there is uniformity of belief regarding the methods of obtaining purity of type. Artificial self-pollination gives uniformity, and continued self-fertilization produces no harmful effects. This method was strongly recommended by officials of the United States Department of Agriculture (Shamel and Cobey, 1907) and by the different state experiment stations. The Howards, in India, likewise urged the use of self-fertilized seed. Garner (1912) states that several types have been inbred by growing the seed under bag from 6 to 8 years without any observable change in vigor or habits of growth. These facts, together with the studies of inheritance of quantitative characters, show that the pure-line theory and Mendel's law furnish a reliable guide to tobacco-breeding operations.

As quality of cured leaf is of such great importance in tobacco, it is necessary that the breeder have a thorough knowledge of the sort of leaf desired. Practical breeding operations must then be carried on under the soil and climatic conditions in which the crop is to be grown. An added complication is the necessity of basing the final judgment of a particular selection upon the comparative value of the cured leaf after fermentation. The difficulties of comparing numerous strains, while not insurmountable, are naturally much greater than for an equal number of small grain selections.

Mutations in Tobacco.—The sudden appearance of giant plants with abnormally high leaf number has been recorded in the Sumatra, Maryland, Cuban, and Connecticut Havana varieties of *N. tabacum* (Allard, 1919). These new forms under field conditions have a much longer period of vegetative vigor than the normal varieties. Consequently, blossoming does not take place under ordinary field conditions.

Otherwise, the general habit of each of these new types is not very different from the normal variety from which it was obtained

Two of these new varieties of giant habit are of some commercial importance. A short account of their first recorded appearance together with their cultivation as commercial varieties will be given. Giant plants were noted in 1912 in the Cuban variety which is grown under shade in the Connecticut Valley (Hayes and Beinhart, 1914). The history of the normal Cuban variety from which the giant type was obtained is of interest (Hayes, 1915). Seed of the normal variety was saved under bag, which insures self-fertilization, from 1904 to 1909, inclusive. In 1910 and 1911 seed was saved in bulk from plants which were grown under the cheesecloth cover used in producing shade-grown tobacco, but individual plants were not bagged. During the period from 1904 to 1910 no abnormal types were observed. Studies of leaf inheritance in the Cuban variety were made from 1910 to 1914, inclusive. An average of 150 plants was carefully examined yearly and no aberrant types were observed

In 1912 about 100 acres were grown by the Windsor Tobacco Growers' Corporation from seed saved in 1911, and late in the season three plants were discovered which had produced a high leaf number and showed no signs of blossoming. One of these plants when taken to the Connecticut Experiment Station greenhouse produced 72 leaves and blossomed about January 1. Considerable seed was saved from this plant and $\frac{1}{3}$ acre of the new type was grown in 1913. The plants were of uniform appearance. They differed from the normal Cuban in having leaves of a somewhat lighter green, in having but few basal suckers, and in a long-continued period of growth; whereas the normal Cuban variety bears a terminal inflorescence after producing from 14 to 25 leaves on the main stem.

This variety was grown commercially for several years but has been discontinued because it is not equal in quality to the normal Cuban variety. A similar type occurred in a Japanese variety (Tukada and others, 1923) and in experimental tests proved fairly satisfactory except for the difficulty of producing seed. This difficulty may be overcome in part by exposing the plants to "shortened days" and thus hastening the production of blossoms. The experiment which demonstrated this fact will be briefly described after giving a short history of Maryland Mammoth.

The Maryland-Narrowleaf-Mammoth type first appeared in 1907 in the second generation of a cross between two common varieties of Maryland tobacco (Garner, 1912). One hundred and fifty-seven plants of this new form were grown in 1908 and all plants were of Mammoth habit. This new variety has been grown commercially since that time and retains its characteristics of high leaf number and non-blooming

habit under normal field conditions.¹ Accurate information regarding the acreage of Mammoth tobacco in southern Maryland is not available but some hundreds of acres were grown in 1920. The chief limiting factor in the acreage is the quantity of seed available. As Maryland tobacco is harvested by cutting and spearing the stalk, there is little additional cost in harvesting the giant type. The Mammoth variety will yield 2,000 pounds or more per acre and the quality of cured leaf is superior to the ordinary varieties. Comparative yields show that the Mammoth variety yields 20 to 25 per cent more than other varieties when grown on productive soil. As the Mammoth variety has shorter internodes than ordinary varieties the leaves shade one another. This prevents coarse texture and dark colors even on highly productive soil. The ordinary varieties, when grown on rich soils, yield dark-colored and coarse-textured leaves. The value per acre of the Mammoth tobacco is 30 to 40 per cent higher than ordinary varieties (see Fig. 42).

Garner and Allard (1920) have studied the effect of relative length of day on growth and development of plants, particularly with respect to sexual reproduction. By placing a ventilated, dark chamber in the field the relative number of hours of exposure to sunlight was controlled as desired. They found that:

Normally the plant can attain the flowering and fruiting stages only when the length of day falls within certain limits, and, consequently, these stages of development ordinarily are reached only during certain seasons of the year. In this particular, some species and varieties respond to relatively long days, while others respond to short days, and still others are capable of responding to all lengths of the day which prevail in the latitude of Washington where the tests were made.

In the absence of a favorable length of day for bringing into expression reproductive processes in certain species, vegetative development may continue and thus lead to the production of such varieties as Stewart Cuban and Maryland Mammoth which under ordinary conditions never reach the flowering stage.

Thus, certain varieties or species may act as early or late maturing, depending simply on the length of day to which they happen to be exposed.

The Stewart Cuban and Maryland Mammoth varieties of tobacco, as well as several other species were used in a determination of the effect of reduced length of day in forcing flowering. In discussing the effects of controlling light as a means of forcing flowering in Maryland Mammoth, Garner² says:

¹ Information kindly furnished by Dr. W. W. GARNER, Physiologist, in Charge of Tobacco and Plant Nutrition Investigations, Bureau of Plant Industry, United States Department of Agriculture.

² From a letter written Sept. 14, 1920.



FIG. 42.—Field of Maryland Mammoth in Prince George's County, Maryland, 1920. The man in the foreground is more than 6 feet tall. Two men of average stature standing in the tobacco are scarcely visible. The stake is 7 feet tall. (Courtesy of Garner.)



FIG. 43.—Control series of Maryland Mammoth tobacco in twelve-quart buckets left out of doors during the experiment. Flower buds just beginning to show when photographed, August 19, 1919. (*Courtesy of Garner.*)



FIG. 44.—Front row in twelve-quart buckets exposed to light from 9 a.m. to 4 p.m. or 7 hours daily. Rear row in twelve-quart buckets exposed to light from 6 a.m. to 6 p.m. or 12 hours daily. Note that latter are larger plants but flowered considerably later than the former. (*Courtesy of Garner.*)

Under a given length of day favorable to flowering, this type can be made to produce any quantity of seed ranging from a single pod up to a large inflorescence by appropriate regulation of the quantity of soil in which the plant grows.

Plants grown in 12-quart buckets produced large amounts of seed when the length of day was shortened by placing the plants in the dark chamber for a part of the normal day. A control series left out of doors during the experiment began to show flower heads about the middle of August (see Fig. 43). Plants exposed to 7 hours of light daily produced large quantities of seed while those exposed to 12 hours of light daily grew larger but were later in blossoming (see Fig. 44).

In southern Florida during the ordinary winter months, the Maryland Mammoth behaves as ordinary tobacco, showing no evidence of its tall, late habit. Thus quantities of seed could easily be produced under these conditions.

Allard (1919) crossed normal varieties with the Mammoth type. The F_1 averaged somewhat higher in leaf number than the normal varieties but invariably blossomed under field conditions in practically the same period as ordinary varieties of *N. tabacum*. A total of 1,820 F_2 plants was grown and 439 were of the giant habit.

CHAPTER XIV

COTTON AND SORGHUM

COTTON

Little is definitely known of the antiquity of cotton. Evidence has been obtained which indicates that it was cultivated in India in 1500 B.C. and in Egypt 1,300 years later. Species of cotton are indigenous both to tropical America and to India. Because of the extent of natural crossing (5 to 13 per cent according to Balls, 1912; 12 to 28 per cent according to Kearney, 1923*b*), the difficulties of studying inheritance and of carrying on practical breeding operations are greater than with many other crops. This crop belongs to the often cross-pollinated group although artificial self-pollination may be easily carried on without apparent reduction in vigor (Kearney, 1923*b*). It seems reasonable to conclude that deterioration in a selected variety is largely the result of natural crossing. Methods of pedigree-seed production should, therefore, be developed to their highest possible efficiency.

Classification.—Cotton belongs to the genus *Gossypium* which is made up of a number of species. Although several classifications of this crop have been published, considerable disagreement still exists. The varieties of cotton grown in India are derived principally from *G. herbaceum*, those grown in Egypt from *G. barbadense*, and those grown in America from *G. hirsutum* and *G. barbadense*. Among the classifications of cotton that have been made those of Parlatore (1866), Todaro (1877), and Watt (1907) may be mentioned. In addition to these, Gammie (1905) has published a classification of the Indian cottons and Duggar (1907) a classification of the varieties of American Upland cotton. The commercial value of cotton and the separation into the above species groups are largely determined by three characteristics of the fiber, namely, length, tensile strength, and fineness. Some other morphological characters that have been used in classification are: presence or absence of fuzz on the seed, color of fiber and flower, form of boll, and general habit of growth.

Species, Relationship, and Chromosome Number.—Webber (1905) was unable to cross Aiden cotton which he classified as *G. herbaceum* with varieties of either Sea Island, *G. barbadense*, or Upland, *G. hirsutum*. On the other hand, successful crosses have been made between varieties belonging to the two species last named. The reason for this difference

in behavior may be owing to a difference in chromosome number and what it involves. In this connection Denham (1924) has published some interesting results on the cytology of the cotton plant. Thirty-two varieties belonging to American, Sea Island, Egyptian, Indian, and Chinese types were examined for chromosome number and were found to fall into one of two groups. The haploid number of chromosomes for the Indian and Chinese types was found to be 13 and the haploid number for the other types 26. In the group with 13 chromosomes, one was found to be distinctly larger than the remaining 12 and in the other group two chromosomes were found to be distinctly larger than the remaining 24. Denham states that on the whole the plants of the 26-chromosome group are larger, stems taller, leaves, flowers, and bolls larger and lint longer than in the plants of the 13-chromosome group. It is suggested that this may be an instance of gigantism owing to the doubling of the chromosome number. As far as is known no successful crosses have been made between the American or Egyptian types of cotton and the true Indian type.

Inheritance Studies.¹—The transmission of characters in cotton have been studied by several plant breeders. In general, the behavior of the characters of this crop is in conformity with Mendelian principles.

Leaf-blade Color.—Leuke (1911) made several crosses involving red- and green-leaved types in which he found red dominant and obtained monohybrid segregation in F_2 . Considerable variation was manifest in the intensity of the red coloring. As a result of crosses between varieties of Upland cotton with red and green leaves, McLendon (1912) concluded that the F_1 was intermediate and that the F_2 generation indicated a 1:2:1 segregation. In a cross between a broad-lobed, red-leaved form and a narrow-lobed, green-leaved form the F_1 was intermediate with respect to both characters and the segregation in the F_2 generation was characteristic of a dihybrid when the two characters are inherited independently and when it is possible to distinguish the intermediates.

Leaf-callus Color.—Balls (1910) studied the inheritance of coloring on the leaf callus in an Upland-Egyptian cross. In F_1 an intermediate condition was obtained and by classifying the F_2 generation as "spotted," "intermediate," and "no spot" a close approximation to a 1:2:1 ratio was obtained. The "spotted" and "no spot" bred true in F_3 and the "intermediate" segregated again.

Petal Color.—In a cross between a red- and a yellow-flowered Indian cotton, Fletcher (1907) obtained evidence that these characters were dependent on a single factor difference for their expression and that red was dominant to yellow. In another cross he found that yellow was dominant to white. Fyson (1908) obtained similar results in a yellow-white cross with Indian cotton. Evidence of monohybrid segregation was obtained in the F_2 generation. Balls (1910) on the other hand, in an F_1 hybrid between Upland and Egyptian, found that petal color was intermediate and in F_2 he obtained yellow, intermediate, and white flowers in the ratio of 1:2:1. In a later publication (1912) it is suggested that there are at least three pairs of allelomorphs involved in the inheritance of petal color in the Upland-Egyptian crosses. In the work of Balls as well as that of Kearney (1923a) with the yellow-white cross there was

¹ A summary of KEARNEY (1923a) has been freely used in this discussion.

an excess of the light-colored petal types obtained in F_2 . Kearney crossed Holdon (Upland) with Pima (Egyptian). Leake (1911) obtained an F_2 generation from a cross of two Indian cottons one of which was yellow-flowered the other white-flowered, in which segregation was nearer 2:1 than 3:1. It is suggested that the ratio obtained is owing to the fact that Indian white-flowered strains are harder than the yellow-flowered strains. The same investigator found a correlation between size and color of petal, white petals being smaller than yellow petals. Kearney obtained similar results in the Holdon-Pima cross, however, individual F_2 plants were found in which the reverse relation existed. These F_2 plants bred true in F_3 which indicates that the correlation was a result of genetic linkage.

Leake obtained some evidence that red color in the vegetative organs and in the petals may be dependent on the same factor for its development. In the F_2 generation of a cross of red-leafed, red-flowered with green-leafed, yellow-flowered Indian cotton, he obtained for both characters a ratio of 3 red:1 non-red. In another case he crossed a red-leafed, red-flowered type with a green-leafed, white-flowered type.

In F_2 the following were obtained:

	NUMBER
Petals, red; leaf all red.....	89
Petals, red and yellow; leaf veins red.....	193
Petals, red and white; leaf all red.....	30
Petals, red and white; leaf veins red.....	78
Petals, yellow; leaf green.....	96
Petals, white; leaf green.....	25

The results were explained by assuming that the red-colored parent carried both a factor for red color in the leaf and petal dominant to its absence and a factor for yellow color in the petal dominant to its absence. The other parent carried the recessive factors for both of these colors. McLendon (1912) and Harland (1920) have also investigated the inheritance of flower color in cotton. The latter obtained a deviation from the expected F_2 classes which was explained on the basis of accidental cross-pollination.

Petal Spot.—McLendon crossed Sea Island cotton which had spotted petals with varieties of Upland which were spotless. The F_1 was intermediate and the F_2 indicated that a single-factor difference was operative. In a cross between Holdon and Pima, Kearney (1923a) obtained similar results except that the presence of the spot behaved as a dominant over its absence. Balls (1910) obtained some evidence from an Upland-Egyptian cross that there may be two allelomorphic pairs concerned in the inheritance of petal spot. Leake and Prasad (1914) found that the presence of this character was completely dominant to its absence in the F_1 of a cross between Chinese cotton.

Anther Color.—The inheritance of anther color has been investigated by Kearney, Balls, and McLendon. The results obtained indicate that this character is transmitted as a simple monohybrid with yellow dominant to the pale color. McLendon's results with Sea Island-Upland crosses seemed to indicate that petal and anther colors were controlled by the same factor, on the other hand, in the Holdon-Pima cross made by Kearney the inheritance of color in these two organs was independent.

Fiber Color.—Fiber color differentiated the Holdon (white) and Pima (pale buff) parents in the cross made by Kearney. The F_1 generation was intermediate and in F_2 a unimodal curve was obtained. In a cross between Mit Afifi Egyptian (brown fiber) and a white-fibered Upland cotton, Balls (1910) obtained an intermediate F_1 and a segregation in F_2 which indicated that a single factor difference was operative

in the inheritance of this character. In a later publication (Balls, 1912) there was some evidence offered that fiber color was somewhat more complex in its inheritance.

Petiole Hairiness.—In an Upland-Egyptian cross, Balls (1910) found that pubescence on the petiole was inherited as a simple monohybrid with the glabrous condition dominant. In a subsequent publication (1912) the same investigator presented evidence that the inheritance of this character was somewhat more complicated. Kearney (1923a) in a Holdon-Pima cross found a partial dominance in F_1 of the glabrous condition. In F_2 a skew distribution and transgressive segregation were obtained. In an Upland-Sea Island cross McLendon (1912) obtained incomplete dominance in F_1 of the hairiness of the Upland parent and in F_2 a distribution that ranged from one parent to the other.

Boll Lock Number.—The inheritance of number of locks to the boll seems to be controlled by multiple factors. In a Holdon-Pima cross Kearney obtained an intermediate condition in F_1 and a fairly symmetrical unimodal distribution in F_2 . Balls obtained similar results in crosses between Upland and Egyptian varieties.

Boll Shape.—McLendon investigated certain Sea Island-Upland hybrids and concluded that the short thick type of boll is a recessive character and that it is transmitted as a monohybrid. On the other hand Kearney with a Holdon-Pima cross and Balls with Upland-Egyptian crosses found that the inheritance of boll index (diameter relative to length) was dependent on several factors.

Boll Surface.—Both McLendon and Balls obtained evidence that the inheritance of the character of the surface of the boll (smooth or pitted) was dependent on multiple factors. In a Holdon-Pima cross Kearney found that the presence of the midlock furrow in the Holdon parent was inherited as a dihybrid. Midlock furrow was absent in the Pima parent. In F_2 , 94 plants showed no trace of the furrow whereas the 87 remaining plants showed this character in varying degrees.

Fiber Length.—Balls obtained evidence from Upland-Egyptian hybrids that long fibers were dominant to short and that this character was dependent on a single-factor difference for its expression. The investigations of McLendon and Kearney indicated that fiber length was dependent on several factors. Thadani (1925), in crosses between long- and short-staple forms, obtained evidence that long staple was dominant over short. The same investigator obtained results that indicated a high percentage of lint was dominant to a low percentage. The F_2 and F_3 generations showed that a single-factor difference was involved in the inheritance of this character.

Seed Fuzziness.—The inheritance of the fuzziness of the seed in cotton appears to be controlled by several factors. This character has been investigated by Kearney (1923b), Fletcher (1907), Pyson (1908), Balls (1909, 1910, 1912), and McLendon (1912). In a Holdon-Pima cross entire fuzziness of the upland parent was dominant to partial fuzziness of the Egyptian parent. In another cross between smooth-seeded tree cotton, *G. peruvianum*, and a fuzzy-seeded American Upland variety the smooth-seeded condition was dominant. In a cross between a fuzzy-seeded Upland cotton and a variety of Egyptian with very little fuzz on the seed, Balls obtained a dihybrid ratio, 15:1, in F_2 . In crosses between varieties of Egyptian cotton differing in the amount of fuzz on the seed, monohybrid segregation was obtained in F_2 , more fuzz being dominant over less fuzz. Thadani (1925) found that naked seed in the Upland variety, No Lint, was completely dominant over fuzzy seed in other Upland varieties. The segregating ratios obtained indicated that a single-factor difference was operative in the inheritance of these characters.

Leaf Shape.—Kearney (1923a) investigated the inheritance of leaf index (width as a percentage of the length) and leaf-lobe index (distance to the upper sinus as a percentage of the length) in a Holdon-Pima cross. In F_1 the mean leaf index was higher than

in either parent whereas the mean leaf-lobe index was like that of Pima the more deeply lobed parent. The distributions for each of these characters obtained in F_2 indicated that multiple-factor inheritance was involved. Balls (1912) obtained similar results with regard to leaf-lobe index in an Upland-Egyptian cross. Leake (1908) studied the inheritance of a "leaf factor" which he obtained by integrating the breadth of the lobes and the depth of the lobation in crosses of *G. indicum* (deep, narrow lobes) with *G. arboreum* or *G. neglectum* (broad, shallow lobes). In F_1 an intermediate condition was obtained and in F_2 a 1:2:1 segregation occurred. Fyson (1908) also obtained monohybrid segregation with respect to this character but he found deep, narrow-lobed leaves dominant. Shoemaker (1909) crossed two Upland cottons, one an "okra leaf" (deep, narrow lobes) type and the other a shallow, broad-lobed type. In F_1 intermediates were obtained and in F_2 a 1:2:1 segregation occurred. McLendon (1912) obtained similar results with a Sea Island-Upland cross.

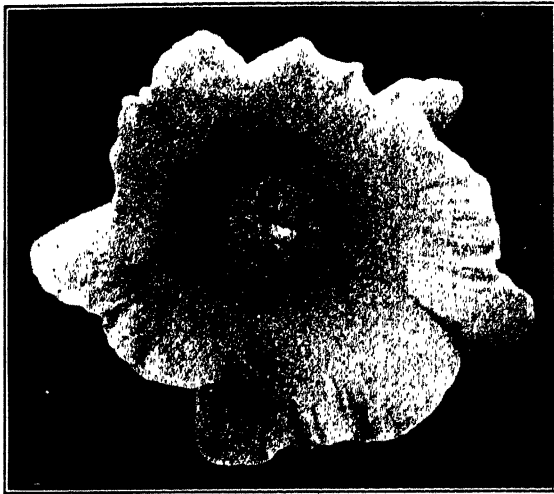


FIG. 45.—View of flower of cotton, from above, showing position of petals, stigmas and stamens (natural size). (After Cook.)

Size Characters.—Kearney (1923a) studied the inheritance of 18 size characters, some of which have been mentioned above. Most of these size characters showed heterosis in F_1 and the distributions obtained in F_2 indicated multiple-factor inheritance. Balls found that a dominant long petal when crossed with a recessive short petal gave in F_2 a 3:1 segregation. The same investigator in a cross between Egyptian (Abassi) and Texas Upland obtained transgressive segregation. Similar results were secured in studying the inheritance of date of flowering and weight of seed. The results of the study of weight of seed are of general interest. In a cross of Afifi and Truitt, where the mean seed weights of the parents were 0.105 and 0.135 grams, respectively, the weight of the F_1 was 0.165 grams. Weights in F_2 varied from 0.08 to 0.175 grams. The light-seeded forms bred comparatively true in F_2 , although differing somewhat in means. The larger-seeded types bred true in F_2 or segregated, giving both large- and small-seeded forms. An illustration of this sort of behavior for the parents, F_1 and F_2 generations, is given diagrammatically in Fig. 47. As has been pointed out, length of lint is also inherited and, in some cases, segregation

approaches a simple 3 : 1 ratio with long lint as the dominant character. Later generations in some crosses gave pure parental types as well as other lint lengths which appeared homozygous. Correlation between length of lint and size of seed may explain some complications



FIG. 46.—Upper left, flower of Upland cotton, from below, with bracts removed showing the arrangement of calyx lobes, petals and nectaries; at right, petals; lower left flower of cotton with one bract removed showing spirally arranged stamens and stigma. (After Cook.)

Chlorophyll Deficiencies.—Stroman and Mahoney (1925) observed two kinds of chlorophyll deficiencies in seedlings of cotton. One of these is described as yellow which contains only a small amount of chlorophyll and the other is described as

ranging from a seedling with small areas devoid of chlorophyll to one which has a small amount of chlorophyll throughout the leaf. The inheritance of the former seems to be dependent on two factors whereas the inheritance of the latter which is called "pattern" seems to be controlled by one, two, and possibly three factors. The ratios 3:1, 9:7, and 37:27 were found in the same and different families. Some evidence was obtained that two of the factors were linked.

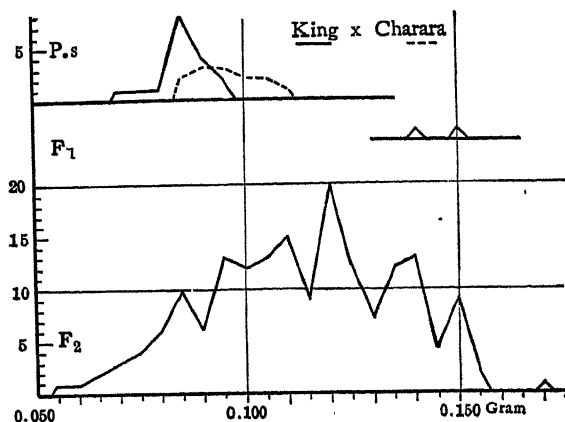


FIG. 47.—Seed weights of parent varieties, King and Charara, and F_1 and F_2 generation crosses. (After Balls.)

Linkage.—In addition to the linkage relations in cotton which have been pointed out above, Thadani (1923), in crosses between varieties of Upland, has found linkage between seed fuzziness and amount of lint on the seed and between vegetative color and fruiting habit. In the crosses reported, naked seed and a low amount of lint were absolutely coupled.

Correlation of Characters.—The correlation of characters is of some interest to the plant breeder. In some cases correlation may be owing to genetic linkage and in other cases the correlation may be purely somatic. Stroman (1925) made a statistical study of 16 varieties of cotton. Positive correlations were found for all varieties between yield of lint and of seed, yield of lint and number of five-lock bolls, yield of seed and number of five-lock bolls, yield of lint and number of four-lock bolls. On the other hand, no consistent correlation was found in the different varieties between yield of lint and per cent of lint, yield and length of lint, yield of seed and per cent of lint, yield of seed and length of lint, per cent of lint and length of lint, and per cent or length of lint and five- or four-lock bolls.

Dunlavy (1923) has reported significant correlations between eight pairs of characters in Texas cotton. Among the characters studied was lint index which is defined as "the weight in grams of the fibers produced by 100 seeds." The correlations obtained were as follows:

Lint index and weight of seed	+0 70 ± 0 02
Boll size and weight of seed	+0 66 ± 0 03
Per cent of five-lock bolls and size of boll	+0 53 ± 0 06
Weight of seed and per cent of lint	-0 53 ± 0 04
Boll size and lint index	+0 48 ± 0 05
Per cent of lint and length of staple	-0 44 ± 0 04
Weight of seed and length of staple	+0 43 ± 0 04
Boll size and per cent of lint	-0 39 ± 0 05

Kearney (1924) found that the degree of the expression of petal spot in Pima cotton was positively correlated with size of flower. It is suggested that this character may be of importance in roguing pure seed stock. Harris, *et al.* (1924) have pointed out that the tissue fluids of Egyptian varieties of cotton carry a higher chloride content than do those of the Upland varieties. This may partly explain why the Egyptian sorts give better results on saline types of land.

Kearney (1924c) has pointed out that the bolls on the lower parts of the plant produce the shorter fibers; hence, the later "pickings" yield the longer fibers. Length of fiber has been found (Prasad, 1922) to be correlated with length of stigma. It is suggested that this relationship may be owing to genetic linkage.

Selective Fertilization.—Kearney (1923a) applied both Pima and Upland pollen separately to different flowers of Pima and found that the pollen tubes developed with equal rapidity. On the other hand, when a mixture of pollen was applied to an Egyptian flower, selective fertilization occurred in favor of the related pollen. This differential in favor of the related pollen was obtained irrespective of whether the pollen mixture consisted of a mixture of pollen from different varieties of Egyptian or of a mixture of pollen from Egyptian and Upland. Kearney states that the selective fertilization may be owing to an inhibitive influence of pollen of the same variety upon foreign pollen. In a later paper (1924a), the same author reported the results of further study on this question. It was found that on the average about 75 per cent of the ovules were fertilized by pollen of the same type and variety when pollen of the other type was used simultaneously and in equal quantity. This held true for both the Egyptian and the Upland types.

Mutations in Cotton.—The cotton plant, like *Oenothera*, has often been spoken of as having germinal instability and likely to produce mutations. While mutations undoubtedly do occur, it is likewise highly probable that many of the so-called mutations are simple segregates of a former natural cross. The ease with which natural crossing occurs and the large number of chromosomes contained in the cotton gamete facilitate the appearance of forms differing from the general type. Egyptian cotton is described by Kearney (1914) as being a mutating type. From it the varieties Yuma, Pima, and Gila are supposed to have arisen.

In this connection it is of interest to point out that the common belief as to the origin of Egyptian cotton is that it arose by hybridization between a brown-linted tree cotton and American Sea Island. The subsequent development is unknown.

In view of the foregoing, and the fact that no convincing evidence has been presented to the contrary, the present writers believe that many of these supposed mutations are in reality factorial recombinations resulting from natural crossing.

Cotton Breeding.—Cotton improvement by breeding may be sought along lines similar to those followed with naturally selfed crops. In producing pure-line material for scientific study and subsequent hybridization, it is essential to obtain absolute self-pollination. It has been pointed out above that continued self-fertilization in cotton is not attended by a marked reduction in vigor. Evidence in support of this statement has been offered by Kearney (1923b), Harland (1923), and others.

One of the outstanding problems of the cotton industry at the present time is to standardize production. The supply of pure seed available for planting is wholly inadequate. The mixing of seed at the gin and the natural crossing that takes place in the field are two very important causes of the deterioration of superior varieties. These difficulties may be overcome first by obtaining or breeding a superior pure strain and then concentrating community effort on growing this one strain. Uniformity of staple is very important to the manufacturer.

From a commercial standpoint, a productive cotton with long lint and smooth seed is desirable. Webber (1905) crossed Klondike, a productive Upland variety, and Sea Island, which has long lint and smooth seed. Out of an F_2 generation consisting of several thousand plants, only 12 combined the large blunt bolls of the Upland with the long lint and black seed of Sea Island. The progeny of each of these 12 plants was grown in isolated plots and subjected to vigorous selection. In the fifth generation a number of plants gave progeny "nearly fixed in type."

Resistance to wilt disease is a character of considerable commercial importance. This disease is caused by *Fusarium vasinfectum* Atk. which, according to Orton, attacks only the cotton and its near relatives. By the plant-to-row method and under wilt-infection conditions, it was found possible to build up varieties which are resistant to wilt. A number of resistant, high-yielding varieties have been introduced in the cotton-growing regions of the United States. The character of wilt resistance was transmitted in crosses but nearly every cross gave a different result. In general, resistance proved dominant but there was often considerable variability, possibly due to the gametic composition of the parents or to the nature of the reaction between the disease organism and the host plant or to the lack of uniform environmental conditions. Wilt resistance does

occur and varieties may be obtained which are resistant and are also of good quality with respect to yield and staple.

Cotton anthracnose, *Glomerella gossypii*, and bacterial blight, *Bacterium malvacearum*, are other diseases of cotton which may be controlled by the production and use of disease-resistant varieties.

SORGHUM¹

Origin.—The numerous diversified forms of sorghum indicate that it has been cultivated a long time. Evidence has been found that it was grown in Egypt as early as 2200 B.C. Hackel places all the cultivated sorghums and the various forms of Johnson grass in one botanical species. It has been pointed out by Piper (1916) that two species exist: the perennials, Johnson grass and its varieties (*Andropogon halepensis*), and the annual sorghums (*Andropogon sorghum*). The former possesses rootstocks, and it is difficult to cross it with either the cultivated or wild forms of sorghum.

The wild annual sorghums, which are found almost exclusively in Africa, cross readily with the cultivated forms. Piper suggests that one or more of these several wild annual forms may be the ancestor of the cultivated forms. Africa is thought to be the native home of the cultivated sorghums.

In sorghum, as in cotton, there is considerable natural crossing. Complete self-fertilization is readily induced by artificial means and, apparently, it does not bring about a reduction in vigor.

Agricultural Groups and Importance.—On the basis of the four economic characters—production of grain, sugar, forage, and broom straw—four agricultural types of sorghums have been developed. These are: (1) grain sorghums, (2) sweet sorghums, (3) broom corn, and (4) grass sorghum (Sudan grass, Tunis grass, etc.). All four groups are used for forage to some extent. Seeds of the first three groups are used for grain, the sweet sorghums for syrup manufacturing and the broom-corn panicle for making brooms. In India, Africa, and Manchuria grain sorghums are an important source of food for the human inhabitants and in Manchuria stalks of the grain sorghum known as kaoliang are used for fuel and for making baskets, furniture, and mats.

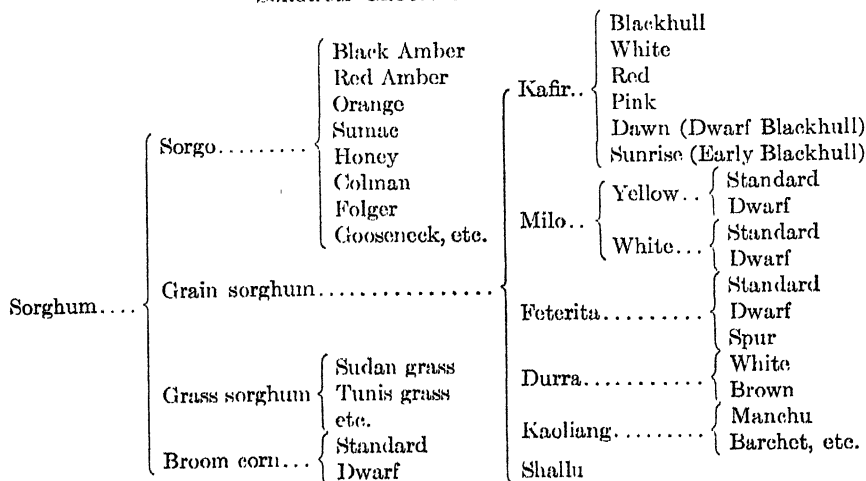
The sorghums are exceedingly important crops in the southern half of the Great Plains area in the United States. In this section the sorghums furnish a large portion of the feed for livestock. They are adapted to hot and dry conditions where corn is not usually successful. The drought resistance of sorghum probably is a result of several factors such as the low-transpiration ratio as shown by Briggs and Shantz

¹ An unpublished paper by J. H. MARTIN, Agronomist of the Office of Cereal Crops and Diseases, United States Department of Agriculture, was used freely in this section.

(1914) and Miller (1923), the large number of feeding roots per plant in proportion to the leaf surface (Miller, 1916), and the faculty of remaining dormant during periods of drought.

Classification.—The main groups of sorghum and some of the principal varieties are given in the following diagram taken from Vinall *et al.* (1924):

SORGHUM GROUPS AND VARIETIES



There are numerous varieties of sorgho differing in height, time of maturity, compactness of panicle, and color of glumes and seed. The varieties of Black Amber, Red Amber, Orange, and Sumac represent the chief types. The grain sorghums belong chiefly to the groups: kafir, milo, durra, feterita, and kaoliang. These groups, except feterita, which is somewhat similar to the durras, as well as sorgho, the broom corns, and the grass sorghums can be distinguished by the following key which is an abridgment of one presented by Piper (1924):

KEY TO VARIETIES OF SORGHUM

- Stems slender (6 millimeters or less); leaves narrow (12 to 30 millimeters) Grass sorghums
- Stems stout (18 to 33 millimeters); leaves broad (40 to 75 millimeters)
- I. Pith juicy
- A. Juice abundant and very sweet.....Sorgho
- B. Juice scanty, slightly sweet to subacid, lemmas awnless.....Kafir
- II. Pith dry
- A. Panicle lax
1. Panicle, 4 to 7 decimeters long; branches greatly elongated..... Broom corn
2. Panicle, 2.5 to 4 decimeters long
- a. Panicle conical; branches strongly drooping.....Shallu
- b. Panicle oval or obovate; branches spreading.....Kaoliang

B. Panicle compact, 1 to 2.5 decimeters long

1. Spikelets elliptic-oval or obovate, 2.5 to 3.5 millimeters wide, lemmas awned
2. Spikelets broadly obovate, 4.5 to 6 millimeters wide
 - a. Glumes gray or greenish; lemmas awned or awnless; grains strongly flattened
 - b. Glumes brown or black, lemmas awned; grains slightly flattened

Kaoliang

Durra

Milo

Inheritance Studies.—Sorghum has not received as much attention by plant geneticists as its economic importance deserves. As compared with corn, the inheritance studies of sorghum have been meager but the work that has been reported indicates that the characters of this crop are inherited in a manner similar to the inheritance of characters in other farm crops.

Color—Graham (1916) of India found that the inheritance of color of seed coats in certain crosses of sorghum to be dependent upon single-factor differences. Red may be allelomorphic to yellow or white and likewise yellow may be allelomorphic to white. Red is dominant to both yellow and white, and yellow is dominant to white. Sometimes when yellow and white are crossed the heterozygote is red and in the next generation segregates with a 9 red:3 yellow:4 white ratio. Graham suggests that certain of the white seeds are undeveloped reds requiring the presence of yellow to cause the development of the red color. Vinnall and Cron (1921) crossed Blackhull Kafir and Feterita with bluish-white and reddish-brown seeds, respectively, and obtained a 9:7 ratio in F_2 . Conner and Karper (1923) crossed Dwarf Yellow with Dwarf White milo and obtained in F_1 seeds that were indistinguishable from the yellow-seeded parent and in F_2 a ratio of 3 yellow-seeded:1 white-seeded form. The F_1 plants of Blackhull \times Red Kafir had pale-red seeds and the F_2 plants gave a segregation of 1 red:2 intermediate:1 white. In F_3 the red- and white-seeded forms bred true whereas the pale red-seeded plants again segregated. The cross Blackhull \times Pink Kafir gave similar results with Pink incompletely dominant. Sielinger (1924) in crosses between Sunrise and Red Kafir and between White and Red Kafir obtained F_2 generations that showed simple monohybrid segregation with red seed dominant to white. In certain other crosses the inheritance of color was somewhat more complex. The following factorial constitutions with respect to seed color were determined:

Feterita and Blackhull kaoliang	$BB\ ss\ rr$
Sunrise and white kafir	$bb\ SS\ rr$
Red kafir	$bb\ SS\ RR$

The factor B in the presence of S produces brown in the nucellar tissue; S produces color in the epidermal layer and its allelomorph when homozygous prevents the formation of brown color in the epidermis; and R is the factor for red color in the epidermis.

In the F_2 of the cross feterita \times red kafir the following phenotypes were obtained in the ratio of brown seed with a brown nucellar layer, 45: white seed with a brown nucellar layer, 3: red and pink seed with no brown nucellar layer, 12: white seed with no brown nucellar layer, 4.

Vinnall and Cron (1921) reported red glumes dominant over black with a single-factor difference.

Ramathan (1924) has also made a study of color inheritance in sorghum. Red pigmentation over the neuters and red color of grains each segregated as monohybrids

in the F_2 generation. An inhibitory factor which prevented the development of black color on the glumes was discovered.

Character of Stalk.—Hilson (1916) found that a pithy stalk was dominant to a sweet stalk and that the inheritance of these characters was controlled by a single-factor difference. Similar results were obtained in Kansas (Swanson, 1923) in a cross between Red Amber and feterita. It was found that the inheritance of a pithy stalk was correlated with a clear-white appearance of the midvein of the leaf and a juicy stalk was correlated with a dull or cloudy appearance of the midvein. In the above mentioned cross not all plants with juicy stalks were saccharine. Pithy stalks, compact heads, and white seed—the combination of characters in the feterita parent were found to be linked in inheritance.¹

Character of Panicle.—In a cross between Kansas Orange and Dwarf Yellow milo made at the Kansas Station it was found that the open-panicled type was dominant over the compact-panicled type. A total of 306 F_2 plants were classed as follows: compact, 31; intermediate, 77; open, 111; and sprangly, 87. The data indicate that the inheritance of this character is dependent on several factors. Similar results were obtained from a cross between Red Amber and feterita. The F_2 generation was classified as follows: very compact, 54; compact, 471; intermediate, 626; open, 822; and sprangly, 653.

Kansas Orange has an erect whereas Dwarf Yellow milo has a recurved peduncle. In the F_1 generation of the above-mentioned cross, the peduncles were more or less recurved but in the F_2 generation there were 291 plants with erect and 15 plants with recurved peduncles. The fact that recurving is influenced greatly by vigor, i.e., the heavier the panicle the greater the tendency for it to become pendant and the further fact that the F_1 generation of the above cross showed hybrid vigor probably explain what appears to be conflicting evidence in regard to the dominance of the erect condition.

Shape of Glume.—Vinnall and Cron (1921) studied the inheritance of glume shape in a cross between Dwarf milo and feterita. Dwarf milo has broad, truncate glumes, whereas feterita has narrow, ovate glumes. The F_1 generation showed that the broad, truncate glumes were dominant. In F_2 , 187 plants with truncate glumes and 64 plants with ovate glumes were obtained.

Glume Hairs.—Rannathan (1924) found that the production and distribution of hairs on the glumes were depended on a number of factors. In general, heavy pubescence behaved as a dominant to the glabrous condition.

Awns.—The same investigators also studied the inheritance of awn development. The glumes of Dwarf milo are awned and those of feterita are not. In F_1 the seeds were not awned and in F_2 183 plants with awnless seeds and 68 plants with awned seeds were obtained. Similar observations were made at the Kansas Station in a cross between Kansas Orange and Dwarf Yellow milo. The F_2 generation of this cross produced 247 awnless and 62 awned plants.

Size Characters.—In addition to the inheritance of the quantitative characters mentioned above, Graham (1916) has investigated the inheritance of length of glumes. Long and short glumes behaved as a simple Mendelian pair with the former dominant.

In the F_2 generation of a cross between Red Amber and feterita at the Kansas Station, 337 plants with small seed, 2,025 with intermediate seed, and 286 with large seed were obtained. This sort of segregation is rather typical of the inheritance of a size character that is dependent upon several factors for its expression.

Chlorophyll Deficiencies.—Conner and Karper (1924) have reported chlorophyll deficiencies in sorghum similar to those found in maize. The seed of a certain Black-hull kafir plant produced green, virescent white, and white seedlings. The seed of

¹ The data from the Kansas Station have not been published and were furnished to the writers by the courtesy of Prof. J. H. Parker.

another plant produced 834 green and 222 white seedlings. The factors involved in the inheritance of these chlorophyll deficiencies have not yet been determined.

Resistance to Smut.—There are several smuts which attack the sorghums but only two of them are of economic importance in the United States. These are covered kernel smut, *Sphacelotheca sorghi*, and head smut, *Sorosporium reilianum*. The former is by far the more prevalent and the more destructive. Reed and Melchers (1925) have reported the varietal resistance of sorghums grown at several places to covered kernel smut. Feterita, four varieties of milo, one variety of kaoliang, and some recent introductions of White durra proved highly resistant to *S. sorghi* whereas all the strains of shallu, the sorgos, the kafirs, Brown and White durra proved highly susceptible. Sudan grass, three varieties of broom corn, and most of the brown kaoliangs showed low or intermediate percentages of infection. The same authors obtained some evidence that the sorghums are less susceptible to *Sorosporium reilianum* than to *Sphacelotheca sorghi*. Feterita, milo, and broom corn showed no infection and the kafirs and kaoliangs only a slight infection to head smut.

Swanson (1923) studied the resistance to kernel smut (*Sphacelotheca sorghi*) in a cross between feterita and Red Amber at Hays, Kan. Feterita was entirely free from smut while the Red Amber produced 17.6 per cent of smut. Nearly 300 F_2 plants were selected at random and were tested in F_3 by the progeny test. There were 214 rows which produced some smut and 72 which were smut free which is a close approximation of a 3:1 ratio. The percentage of smut infection was highest in the F_3 progenies breeding true for pithy stalks which indicates a genetic linkage between the characters of the stalk and reaction to smut.

Breeding Sorghum.—Sorghum belongs to the often cross-pollinated group of farm crops and the essential features of breeding it are the same as for the self-fertilized group. Sorghum, however, is more frequently cross-fertilized than most of the other naturally selfed crops and for this reason it is necessary to resort to bagging the panicles, where different lines are grown in close proximity to one another. That bagging does not inhibit the setting of viable seed is shown by the work of Conner, Ball, Ten Hock, Townsend, and Leidigh, all of whom secured viable seed from panicles so protected. Leidigh (1911) credits Conner with the statement that "a particular strain of Orange sorghum which he grew two generations from seed, bagged each year, possessed extraordinary vitality and vigor and was remarkably pure and uniform." Townsend (1909) obtained similar results. Conner and Karper (1924) after six or seven generations of self-fertilizing sorghums concluded that inbreeding did not cause a reduction or an increase in the size of the head or in productiveness except where it had isolated subvarieties differing from the parent family. Inbreeding fixes type and the type may be good or bad depending on the particular hereditary complex isolated.

One of the ideals sought in sorghum breeding is a form which combines the desirable characteristics of a grain and forage sorghum, *i.e.*, a form which has a juicy stalk and at the same time produces a high yield of seed. Some progress has been made along this line. Sunrise, a selection developed at the Amarillo Experiment Station in Texas, is to some extent a "dual-purpose" sorghum. Considerable work which has for its object the development of this type of sorghum is in progress at the Kansas stations.

Other characteristics, such as resistance to smut, resistance to lodging, resistance to drouth, and early maturity, are important in connection with improving sorghum. The color of seed is also of economic importance. On the market the yellow-seeded forms command the highest price and the brown-seeded forms the lowest.

Deterioration of improved varieties is brought about largely by natural crossing and chance mixing. By means of roguing, chance mixtures and crosses are eliminated and varieties are kept in a pure condition. The isolated seed plot also is recommended as a correct farming practice.

Some Results of Selection.—Sorghum improvement by breeding has been accomplished principally through selection. Dwarf forms have occurred in most varieties and have furnished material for the production of such varieties as Dwarf milo, Dwarf kafir, etc. These varieties have been isolated through selection. Sugar content has also been improved. Failyer and Willard conducted selection experiments at the Kansas Station from 1884 to 1903. During that time they increased the sugar content of the Orange variety from 12.62 to 16.10 per cent. At the Delaware Agricultural Experiment Station even more striking results were obtained (Neale, 1901). The variety Amber, from which selections were made, contained on the average 11 per cent of sugar with a purity of 65. One of the selections made from it had a sugar content of 18.2 per cent with a purity of 81. Dillman (1916), of the United States Department of Agriculture, made several selections from Minnesota Amber with the object of securing an early maturing, drought-resistant strain. One of the selections, Dakota Amber, has proved valuable. It is more dwarf in habit of growth than Minnesota Amber and matures 15 days earlier. It produces excellent forage as well as abundant seed. Early dwarf forms, as a rule, are more drought resistant than late ones.

In addition to the forms mentioned above numerous selections have been made among the sorghums grown in what is commonly known as the sorghum belt of the United States. There is evidence that some of the selections are of hybrid origin due to natural crossing. Among the selections that are grown commercially may be mentioned Sunrise, Schrock, Dwarf Hegari, Spur feterita, Freed, and Darso.

CHAPTER XV

INHERITANCE IN MAIZE

Maize was the most important bread crop of the American Indians and even today is the most important crop in the Western Hemisphere. The Indians brought the culture of maize to a high state of advancement and developed innumerable varieties. On the foundations made by the Indians modern corn breeding has made marked advances, but perhaps no North American varieties are so notable as those developed by the Incas in Peru.

Origin and Species.—It is generally believed that Mexico is the original home of the maize plant, although there is no absolute proof of this (Harshberger, 1897). *Zea mays* L., belongs to the tribe Maydeæ of the order Gramineæ. All varieties of Indian corn are placed in the species *mays*. The nearest relative of maize is teosinte, *Euchlæna mexicana* Schrad. Teosinte and maize cross readily and a natural hybrid between these cultivated grasses was described under the name *Zea canina* by Watson (Harshberger, 1904). A study of these crosses led Harshberger (1904, 1909) to make the hypothesis that maize originated from a hybrid between a sport of *Euchlæna* and normal teosinte. Montgomery (1906) reached the conclusion that maize and teosinte had a common progenitor. It was considered likely that the ancestral form of these cultivated grasses was a large much-branched grass "each branch being terminated by a tassel-like structure bearing hermaphrodite flowers." As evolution progressed, the lateral branches of maize came to bear only pistillate flowers and the central branch staminate flowers. This theory is strengthened by the types of inflorescence which frequently appear in maize varieties. Often the central spike of the tassel of lateral branches bears seeds, while the side branches of the same tassel bear only staminate organs. All gradations appear between the normal ear of maize and the staminate tassel. It is not uncommon in self-fertilized maize races to obtain plants in which the tassel of the main branch bears both male and female organs. These various abnormalities tend to support the hypothesis outlined by Montgomery.

Collins (1912) has supported the hypothesis that maize originated as a hybrid between teosinte and an unknown grass belonging to the tribe Andropogoneæ. This grass is believed to be somewhat like some varieties of pod corn (*Zea mays tunicata*) which produce seeds only in the tassel and are in many essential characters strongly contrasted with teosinte.

These conclusions have been reached after extensive studies of many primitive varieties of maize, teosinte, and hybrids between teosinte and maize. Collins especially emphasizes the fact that "in practically every case where there is pronounced divergence between teosinte and pod corn, maize shows characters of an intermediate nature and these characters are usually variable."

Weatherwax (1918) proposes that *Zea*, *Euchlaena*, and *Tripsacum*, the three closely related American genera of the tribe *Maydeae*, have descended independently from a common ancestral form now extinct. He disagrees with the prevailing theory of the hybrid origin of maize and states that the theory is not in harmony with the facts of morphology. Collins and Kempton (1920b) have crossed the smallest form of maize, Tom Thumb pop, with teosinte and found perfect freedom of recombination in F_2 , and with one or two exceptions no evidence of simple Mendelian ratios. In a study of crosses between maize and teosinte (Kempton, 1924) in which the recessive plant characters, brachytic, crinkled, and ramose, were used, the hybrids segregated in F_2 for all three characters. Crinkled and ramose appeared in approximately 25 per cent of the progeny, as in maize crosses where these characters are concerned, but brachytic appeared in only 12 per cent of the progeny.

Kuwada (1919, abstract by Ikeno, 1920) studied the chromosomes of maize. The chromosomes were found to be of two types, long and short. *Euchlaena* has 10-haploid chromosomes which are long, and *Andropogon* has the same haploid number of short chromosomes. These data support the theory of the hybrid origin of maize as outlined by Collins. Hance (1921) carefully reviewed the studies made by Kuwada and expresses doubt whether or not it was possible, by the methods which Kuwada used, to prove that the sizes of maize chromosomes were of the two definite types characteristic of *Andropogon* and *Euchlaena*, respectively. Longley (1924) studied the chromosomes of maize and maize relatives. *Euchlaena perennis*, *E. mexicana*, *Zea*, and *Tripsacum* were found to have 20, 10, 10, and 35 bivalent chromosomes, respectively, at diakinesis. Certain strains of sugar corn, notably Black Mexican, were found by Kuwada (1919) and Fisk (1925) to differ widely in chromosome numbers while Kieselbach and Peterson (1925) found 10-haploid chromosomes in large numbers of counts, which they made in dent corn. In a paper presented by Randolph at the International Plant Science Congress at Ithaca, in 1926, it was emphasized that there was considerable variation in chromosome numbers in certain inbred lines of maize.

Sturtevant (1899) divided the species *Zea mays* into several groups and considered each of specific rank. It is perhaps somewhat questionable whether any of the groups deserve to be considered as subspecies, the plan followed by East (see East and Hayes, 1911), although the method is a convenient one. A description of the more important groups is given here.

The Pod Corns.—Each kernel of this corn is enclosed in a pod or husks; the ear is enclosed in husks as in other groups. The ordinary type of pod corn is heterozygous while the homozygous type is highly self-sterile and does not produce seed in the lateral inflorescences but in perfect flowers in the tassel.

*The Flint Corns.*¹—The group comprises those varieties with a starchy endosperm in which the soft starch is surrounded by corneous starch. The proportions of soft and corneous starch vary considerably in different varieties.

*The Pop Corns.*²—In this group there is only a small proportion of soft starch in the endosperm and a correspondingly large proportion of corneous starch. Some seeds may be entirely free from soft starch, but there is generally some soft starch surrounding the germ. The group is characterized by the small size of its seeds and ears.

*The Dent Corns.*³—The corneous starch in this group is located at the sides of the seed and the soft starch extends to the summit. The soft starch dries more rapidly than the corneous and this produces the shrinkage which causes the characteristic indentation of the seed.

*The Flour Corns.*⁴—This group is recognized by an almost entire absence of corneous starch. There is no indentation in some varieties and only a slight one in others. The soft-starch content characterizes this group.

*The Sweet Corns.*⁵—“A well-defined species group characterized by the translucent, horny appearance of the kernels and their more or less crinkled, wrinkled, or shriveled condition.” East (1909) presented evidence which shows that the sweet corns are dent, flint, or pop varieties which have not the ability to mature starch normally. The few starch grains produced are small, angular, and imperfect.

The Waxy Corns.—This group is of Chinese origin (Collins, 1909) and is characterized by an endosperm of a waxy nature which results from a carbohydrate of a different form than in ordinary starchy maize varieties.

Inheritance of Characters.—There are 10 pairs of chromosomes in maize and large numbers of character pairs which segregate in simple Mendelian ratios. The technic of crossing is not difficult and several hundred seeds can be obtained from a single pollination.

As much or more information is available regarding the inheritance of special characters as for any other organism except *Drosophila*. For this reason, studies of the genetics of maize are of great importance. Extensive breeding studies are under way with the aim of obtaining

¹ STURTEVANT, *Bull. Torrey Botanical Club*, p. 355, 1894.

² STURTEVANT, *Bull. Torrey Botanical Club*, p. 325, 1894.

³ *Ibid.*, p. 329.

⁴ *Ibid.*, p. 331.

⁵ *Ibid.*, p. 333.

increased yields, greater resistance to insect and fungus attacks, or improved agronomic characters. A knowledge of maize genetics has aided materially in the development of correct breeding principles.

Endosperm Characters.—The characters which differentiate most of the groups of maize are endosperm characters and, therefore, may under certain conditions be immediately modified by cross pollination. The word “xenia” was first used by Focke (1881) to denote the effect which was apparently produced by the action of pollen upon the maternal tissue of the seed. The endosperm of maize was cited as a classical example of such an effect. After the discovery by Guignard (1899) and Nawaschin (1898) that the polar nuclei of the endosperm fuse with the second male nucleus of the pollen grain, De Vries (1899), Correns (1899), Webber (1900), and Guignard (1899, 1901) saw that this furnished an explanation of xenia in maize. From a consideration of inheritance of endosperm characters the following law of xenia may be formulated:

Xenia may result from crossing varieties which differ in a single visible endosperm character. When a character difference is dependent upon a single dominant factor, xenia occurs only when the factor is carried by the male parent, or, when dominance is incomplete, xenia results when either variety is the male. When a character difference is dependent on more than one factor, all located in one parent, and dominance appears complete, xenia occurs only when these differential factors are located in the male; when dominance is incomplete, xenia occurs if the factors are located in either parent. When two varieties have a similar character or a different character expression but contain between them endosperm factors necessary for the production of a new character, xenia occurs when either variety is the male. A summary of the mode of inheritance of the principal normal endosperm characters, given in the following table, is of interest:

TABLE LIX.—SUMMARY OF INHERITANCE OF ENDOSPERM CHARACTERS IN MAIZE

Parental types	F_1	F_2 approximate ratios	
Yellow endosperm \times colorless	Completely dominant or intermediate yellow. Absence of color in cross studied by White	3 yellow:1 colorless 15 yellow:1 colorless 3 white:1 yellow	Correns, 1901 East and Hayes, 1911 White, 1917 Anderson, 1924b Hayes and Brewbaker, 1926
Brown or pale yellow aleurone <i>versus</i> colorless Aleurone color: purple, red, or white	Partially dominant Dominance or partial dominance of color. Dominance of colorless as a result of I , a dominant inhibitory factor	3 brown 1 colorless Ratios indicate 1 to 5 differential factors	Kvakan, 1924 East and Hayes, 1911 East, 1912b Emerson, 1912a, 1918
Starchy (flint, dent, or pop) \times sweet	Starchy	3 starchy:1 sweet	Correns, 1901 East and Hayes, 1911
Waxy (Chinese maize) \times sweet (American maize)	Starchy	Ratios of 9 starchy:4 sweet:3 waxy	Collins and Kempton, 1911, 1914
Starchy \times waxy	Starchy	3 starchy:1 waxy	Kempton, 1919
Flour \times flinty	No immediate effect	Ratio 1 floury:1 flinty seed on each F_1 ear	Hayes and East, 1915

Kvakan (1924) doubts whether or not there are two duplicate factors for yellow in corn and believes that the 15:1 ratios resulted from a mixture of yellow endosperm and brown aleurone seeds. Anderson (1924b) found no evidence of more than a single dark-yellow endosperm type although he did find a pale-yellow endosperm. Hayes and Brewbaker (1926) found that there were two yellows of different intensity, one a pale yellow and the other darker than pale yellow, which were members apparently of the *Bn* group. As the *Y* group is independent from the *Bn* group there is some reason to expect 15:1 ratios in certain cases.

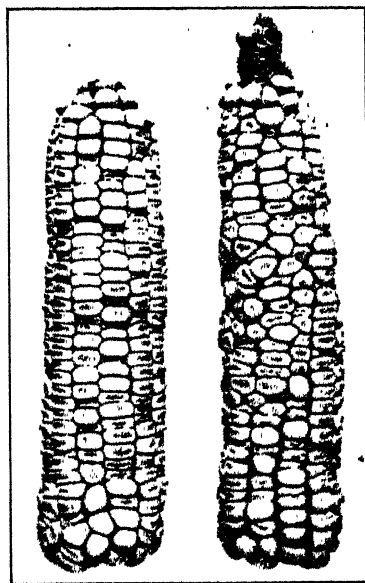


FIG. 48.—Two first year self-fertilized ears of Minn. No. 23 showing the lethal endosperm character.

The inheritance of aleurone color is even more complex than the inheritance of yellow endosperm color. The aleurone may be either colorless, mottled, red, or purple. Three factors are necessary for the production of red aleurone. These Emerson (1918) has called *R*, *C*, and *A*. In addition to these three factors, *Pr*, in either the simplex or duplex condition, gives purple aleurone. An inhibitory factor which was called *I* was first discovered by East and Hayes (1911). When this is present, the aleurone layer is colorless. Races of white corn exist which contain some but not all of the factors necessary for the production of aleurone color. Certain crosses between white races give colored aleurone. With five or six factors involved, it becomes apparent that segregation

in certain cases may be in a simple 3:1 ratio, while segregation in other crosses may give extremely complex ratios. There are various intensities of the purple color in different races. These have been discussed in detail by Emerson (1918). Over waxy or floury endosperm a purple color in the aleurone layer is of a dull-black appearance. With a variation in color of the endosperm from white to dark yellow there is a corresponding variation in color of the aleurone from purple to brownish shades. These differences in aleurone appearance are due to the inheritance of other genetic factors for endosperm characters beside those which govern the ability to produce aleurone color. There are some genetic differences in aleurone colors which are not related to the underlying endosperm characters. Two color patterns have been mentioned by Emerson under the names speckled and dark-capped. The color is found on the crown of the seed and varies from a mere speck to a large spot. Both color patterns are recessive to normal or self-color. Aside from these color patterns which are apparent in homozygous races, there are mottled colors which are only obtained in the heterozygous condition. Emerson has given quite conclusive proof that mottling is associated with the *Rr* factor pair. Apparently endosperms of the constitution *RRR* or *RrR* are self-colored while *Rrr* shows mottling.

The inheritance of an intermediate starchy-sweet (called pseudo-starchy) condition, which is often present in some sweet-corn ears, has been studied by Jones (1919). Three factors were shown to explain the results: (1) a plant factor, *A*, necessary for complete expression of the so-called pseudo-starchy character; (2) an endosperm factor, *B*, which prevents the characteristic shrinking of sweet seeds; (3) an endosperm factor, *C*, determining opaqueness. *C* gives complete dominance, while *A* and *B* give an intermediate condition when heterozygous, and *B* in addition shows a cumulative effect in proportion to the number of factors involved. *C* and *c* give the greatest differential effect only in the presence of the homozygous condition for *A* and *B*. From this brief discussion it is easy to see that reciprocal crosses between *AABBcc* \times *aabbCC* will not give like results. *AABBcc* fertilized with *aabbCC* will give an endosperm condition *ABbCc*, while the reciprocal cross will give *abbCCc*. As *A* is necessary for recognizable expression of pseudo-starchiness, one cross will show xenia while its reciprocal will not. As a rule starchy-sweet crosses are dependent upon a single factor pair.

The cross between the waxy variety of Chinese maize and American sweet varieties is of interest, as maize with a corneous endosperm was obtained in *F*₁, while in *F*₂ a ratio of 9 horny:4 sweet:3 waxy seeds was obtained. Many starchy-sweet crosses have been studied and as yet no case has been obtained which showed more than a single main-factor difference. Apparently, the sugary varieties differ by only a single main factor from the starchy varieties.

Reciprocal crosses between flour and flint showed no immediate effect of cross-pollination. The ears, however, of the F_1 plants showed a distinct segregation into flour and flint seeds in a 1:1 ratio. Later generations showed that the results were most easily explained on the cumulative-factor basis. If a soft flour variety was pollinated by a flint race, the endosperm would contain two factors for soft flour, SS , and one for flint condition, F , or SSF . The reciprocal cross would be FFS . If two factors, FF or SS , are completely dominant over one factor, S or F , respectively, there would be no immediate effect of cross-pollination and the segregation on F_1 ears would be in a 1:1 ratio. Dents crossed with flour races give a very similar result, but the seeds are not so easily distinguished by inspection. Reciprocal crosses between pop and flour races show no immediate effect of pollination with complex segregation on the ears of F_1 plants. Pure flour and pop forms may be obtained in later generations, but the results cannot be explained by a single factor difference. With the hypothesis that pop and flour corns differ by two or more main factors and with each factor behaving in a somewhat similar manner as in the flint-flour cross, the difficulty of a correct classification by inspection is apparent.

It is a well-known fact (East, 1909) that certain sweet-corn varieties, such as Golden Bantam, differ from flint varieties in only a single factor for starch production; other sweet varieties such as Stowell's Evergreen are more like dent corns and when pollinated with pollen from starchy varieties dent seeds result. Jones (1924a) presents evidence that crosses between pop and Cuzco flour corn produce both dent and flint seeds. These various results show that new types may be obtained frequently by variation due to recombination after crossing.

Chlorophyll Inheritance.—The larger numbers of chlorophyll variations which are known to be dependent upon different genetic factors is perhaps one of the most interesting features of the studies of maize genetics. The chlorophyll abnormalities are of two types, those that appear in seedling progenies and those in the mature types. The seedling types are frequently lethal.

Lindstrom (1918) presented an interesting paper upon the mode of inheritance of chlorophyll variation which is summarized here in considerable detail. Three seedling types were observed: white, virescent white, and yellow. The white form is a true albino, apparently lacking chloroplasts. The virescent white appears white at first, but under favorable conditions it gradually becomes a yellowish-green color, especially at the tips of the leaves. There is considerable variation in the appearance of different seedlings of this type but genetically all behave alike. The yellow type gives seedlings with a yellow color. Both the white and the yellow seedlings die before maturity.

The normal green form behaves as an allelomorph to the various seedling abnormalities and contains the three dominant genes, *W*, *V*, and *L*. Counts of the number of normal green plants and the three seedling types obtained from various heterozygous plants are as follows:

Green	1,513	White	555
Green .	4,297	Virescent white	1,394
Green.	1,493	Yellow	532

Virescent whites which turned green on maturity were selfed and produced a progeny consisting of 717 virescent-white seedlings and 9 green. The latter were due probably to stray pollen.

From a study of interrelation of these various factors, Lindstrom has concluded that the following phenotypic formulas explain the appearance of different sorts of seedlings:

GREEN	VIRESCENT WHITE	YELLOW	WHITE
<i>LVW</i>	<i>LvW</i>	<i>lwW</i>	<i>LVw</i>
<i>lvW</i>		<i>lvw</i>	<i>Lvw</i>
		<i>lw</i>	

In a later paper Lindstrom (1925a) has discovered another factor for yellow which produces yellow seedlings when in the homozygous recessive condition and in the presence of *W* in the dominant condition.

These studies have considerable bearing on the present conception of inbreeding and cross-breeding as applied to corn improvement. Lindstrom found, for example, that plants containing the *wW* combination were less vigorous than *WW* forms. As a rule, a *Ww* plant produced only a single stalk which was easily blown over in a strong wind.

There are also abnormal chlorophyll types which appear in the mature plant. Of these, golden, green-striped, fine-striped, and japonica types are simple Mendelian recessives to normal green. In the golden type, when a month or more old, the green color begins to disappear. The golden type is not very vigorous toward maturity. It produces abundant pollen and small ears. The green-striped form appears about 2 months after germination. These stripes are uniform in distribution, green and lighter areas alternating, and running parallel through the leaf. Mature green-striped plants are less vigorous than normal green forms and the leaves wilt more severely on hot days. The japonica types are striped with green, pale yellow, yellow, and white, and are well known, being frequently used for ornamental planting. These forms are more vigorous than the golden or green-striped types. There are also fine-striped and spotted forms. The spotted forms have not as yet been studied thoroughly.

Four of the mature-plant chlorophyll types have been found to be recessive to the normal green forms. The following genetic factors have been used by Lindstrom:

g—golden type
st—green striped
j—japonica
f—fine striped

The following summary expresses the factorial condition of these forms of chlorophyll abnormality;

CHLOROPHYLL TYPES	CHLOROPHYLL FACTORS
Green.....	<i>WVLGstJF</i> or <i>WVlgStJF</i>
White.....	<i>wVLGstJF</i>
Virescent white.....	<i>WvLGstJF</i>
Yellow.....	<i>WvlgStJF</i>
Golden.....	<i>WVLgStJF</i> or <i>WVlgStJF</i>
Green-striped.....	<i>WVLGstJF</i>
Japonica white-striped.....	<i>WVLGstjF</i>
Japonica yellow-striped.....	<i>WVLGstjF</i>
Fine striped.....	<i>WVLGstJf</i>

As will be pointed out in the list of factors, there are at least eight different factors for virescent seedlings and eleven for white seedlings. By examining the linkage relations it will be observed that the loci of several of these factors has been determined. Certain factors, such as *w*₁, produce white seedlings when recessive. Others, such as *w*₅ and *w*₆, are complementary and both must be recessive and homozygous in order that white seedlings may be obtained. Thus *W*₅ and *W*₆ are duplicate genes for chlorophyll, either alone leading to the production of chlorophyll. If *w*₅ and *w*₆ were not linked the progeny of a plant in which both *W*₅ and *W*₆ are heterozygous would be expected to consist of a ratio of 15 green seedlings:1 white. Lindstrom (1924) has presented data regarding three factor pairs, *W*₁*w*₁, *W*₂*w*₂, *W*₃*w*₃, which are inherited independently. All three dominant factors are necessary for the production of chlorophyll but a single factor pair, when homozygous and recessive, leads to the production of white seedlings. In addition to these types which have been mentioned in some detail, there are numerous other types of chlorophyll abnormalities which occur both in seedlings and in mature plants. The extreme complexity of the inheritance of chlorophyll is of interest in relation to the complexity of chlorophyll from a chemical standpoint. Apparently, many different loci play a part in the development of chlorophyll.

Linkage in Maize.—Maize has been used extensively in a study of the chromosome theory of heredity. Without doubt, as much is known for

maize regarding linkage relations as for any other organism except *Drosophila*. Dr R. A. Emerson of Cornell University has been an active leader of the studies of genetics with maize. Other plant-genetics departments have also engaged actively in studying the inheritance of characters. New characters which can be used in linkage studies are being constantly discovered. It is the present purpose to summarize the more important genetic factors which have been discovered together with their linkage relations and to review briefly the inheritance of those characters which are of special interest to the breeder.

An alphabetic list of some of the more important factors, a brief statement of the character concerned and the investigator who described the character will be given. In this list the dominant factors are capitalized:

- A* anthocyanin, general plant color found in aleurone, pericarp, stems, leaves, etc. (Emerson, 1918, 1921*b*)
- ad* adherent, leaves and tassel adhering (Kempton, 1921*b*)
- an* anther ear, semidwarf plant with anthers throughout ear (Emerson and Emerson, 1922)
- B* "brown," a plant color factor. One of an allelomorphous series *B*, *B^w*, *b* (Emerson, 1921*b*)
- br* brachytic, characterized by shortened internodes (Kempton, 1920)
- bl* blotched leaf (Emerson, 1923)
- Bn* Brown aleurone (Kvakan, 1924)
- bv* brevis, dwarf plant (Kvakan lists as "unpublished data," 1924)
- C* colored aleurone, complementary to *A* and *R* factors (East and Hayes, 1911; Emerson, 1918)
- cr* crinkly leaf (Emerson, 1921*a*)
- d* dwarf plant with anthers throughout ear (Emerson and Emerson, 1922; Demerec, 1926*b*)
- de₁* to *de₁₄* defective, partial development of endosperm (Jones, 1920; Lindstrom, 1923*c*; Mangelsdorf, 1926)
- f* fine-striped leaf (Lindstrom, 1918)
- fl* floury endosperm (Hayes and East, 1915)
- g₁* *g₂* golden plant color (Lindstrom, 1918; Jenkins, 1926)
- gl₁* to *gl₄* glossy seedlings (Brunson, 1926; Kvakan, 1924; Hayes and Brewbaker, unpublished)
- gm* germless seeds (Demerec, 1923*a*)
- gs* green-striped leaf (Lindstrom, 1918)
- I* inhibitor of aleurone color (East and Hayes, 1911)
- in* intensifier of red and purple aleurone (Fraser, 1924)
- j* japonica-striped leaf (Lindstrom, 1918)
- l₁*, *l₂* luteus (yellow) seedling. Factors for xanthophyll and carotin pigments (Lindstrom, 1918, 1921, 1925*a*)
- lg* liguleless leaf (Emerson, 1912)
- li* lineate leaf (Collins and Kempton, 1920*a*)
- m₁*, *m₂* yellowish-white seedlings (Stroman, 1924*b*)
- P* pericarp and cob color. An allelomorphous series *P^{rr}*, *P^{wr}*, etc. (Emerson, 1911)
- pb₁* to *pb₄* piebald seedlings (Demerec, 1926*a*)

- pg*₁ to *pg*₅ pale-green seedlings (Brunson, 1924; Demerec, 1925)
- pk* polka dot leaves (Eyster, 1924c)
- Pl* purple plant color, develops in local darkness (Emerson, 1921b)
- pm*₁, *pm*₂ primitive sporophyte (Eyster, 1924a,b) Mangelsdorf (1926) has found several factors for premature germination, *i.e.*, Eyster's primitive sporophyte and lists these as *ge*₁ to *ge*₅.
- Pr* purple aleurone (East and Hayes, 1911), in presence of *A*, *C* and *R*.
- R* "red" aleurone, one of the complementary factors (*ACR*) for aleurone color, and also in an allelomorphic series affecting plant colors and pericarp: *R*^r, *R*^g, *r*^r, *r*^g *r*^{ch}, etc. (East and Hayes, 1911; Emerson, 1918, 1921b)
- ra* ramosa ear (Gernert, 1912)
- sc* scarred endosperm (Eyster, 1922c)
- sh* shrunken endosperm (Hutchison, 1921)
- sk* silkless (Jones, 1925)
- sm* salmon silks (Anderson, 1921)
- su* sugary endosperm (East and Hayes, 1911)
- T* teopod tassel (Lindstrom, 1925b)
- ts*₁ to *ts*₄ tassel seed. Produces only pistillate flowers in the tassel (Emerson, 1920, and unpublished data)
- Tu* tunicate ear (East and Hayes, 1911; Collins, 1917)
- tw*₁ to *tw*₃ twisted seedlings (Kvakun, 1925)
- v* virescent seedlings (Lindstrom, 1918)
- v*₁ to *v*₅, *v*₈ virescent seedlings (Demerec, 1924)
- w*₁ to *w*₃ white seedlings (Lindstrom, 1918, 1923a, 1924)
- w*₂ white seedlings (Stroman, 1924a)
- w*₃ to *w*₁₁ white seedlings (Demerec, 1923b, 1926b)
- wl* white base leaf characters (Stroman, 1924b)
- wx* waxy endosperm (Collins, 1909)
- Xn*₁ xantha seedlings (Trajkovich, 1924)
- Xn*₂ xantha seedlings (Demerec, 1925)
- Y*₁ yellow endosperm (East and Hayes, 1911; Anderson, 1924b)
- Y*_p pale-yellow endosperm (Hayes and Brewbaker, 1926)
- Y*₂ yellow endosperm (Hayes and Brewbaker, 1926)
- zg* *z* zigzag culm (Eyster, 1920, 1922b)

Other genetic factors have been discovered and new factor relations are constantly being determined. Those given in the list are the more important which have been used in studies of linkage relations. A few others have been included because of special interest in the characters concerned.

A summary will be given here of the linkage groups and reference will be made to the investigator concerned. Crossing-over percentages will be given. The chromosome map can be drawn by the student when sufficient information is available, in the light of the information here given:

THE "C" GROUP, *pk*, *C-I*, *sh*, *wx*, *v₁*

Investigator	Factors concerned	Crossing-over percentage
Biegger, 1918	<i>C-wr</i>	26.7
Hutchison, 1921	<i>C-wr</i>	21.7
Stadler, 1925, 1926	<i>C-w₁</i>	17.9-25.9
Hutchison, 1921, 1922	<i>C-sh</i>	3.1-3.4
Stadler, 1926	<i>C-sh</i>	Male gametes 3.4
Stadler, 1926	<i>C-sh</i>	Female gametes 2.3
Eyster, 1924c	<i>C-ph</i>	2
Demerec, 1924	<i>C-v₁</i>	30
Hutchison, 1921, 1922	<i>I-sh</i>	3.6-4.0
Hutchison, 1922	<i>I-wx</i>	26.6
Eyster, 1924c	<i>pk-sh</i>	10
Demerec, 1926b	<i>sh-w₁₁</i>	22.3
Hutchison, 1921, 1922	<i>sh-wr</i>	18.3-21.8
Stadler, 1926	<i>sh-wx</i>	Male gametes 22.1
Stadler, 1926	<i>sh-wx</i>	Female gametes 20.0
Demerec, 1924	<i>v₁-wr</i>	7
Hutchison, 1922	<i>C-I</i>	Closely linked or identical loci
Demerec, 1926b	<i>d_s-sh</i>	22.8

THE "R" GROUP, *R*, *pg₁*, *l₁*, *w₂* (LINDSTROM), *g₁*, *l₁*

Investigator	Factors concerned	Crossing-over percentage
Lindstrom, 1918	<i>R-g₁</i>	23
Brunson, 1924...	<i>R-pg₁</i>	23.3
Lindstrom, 1918, 1921	<i>R-l₁</i>	0-1.6
Demerec, 1926b	<i>R-gm₂</i>	31.0
Lindstrom, 1925a	<i>R-l₁</i>	33.9-35.4
Lindstrom, 1918	<i>l₁-g₁</i>	19
Lindstrom, 1925a	<i>l₁-df</i>	none
Lindstrom, 1925a	<i>l₁-w₂</i>	21.7
Stroman, 1924a...	<i>R-w₂</i>	17
Brunson, 1924...	<i>pg₁-l₁</i>	44.6

THE "su" GROUP, *su*, *Tu*, *de*, *v₈*, *de₁*, *vl*, *de₈*, *ge₁*

Investigator	Factors concerned	Crossing-over percentage
Jones and Gallastegui, 1919	<i>su-Tu</i>	8.3
Eyster, 1921, 1922a	<i>su-Tu</i>	28.6-29.6
Demerec, 1926a	<i>su-v₈</i>	32.4
Wentz, 1925...	<i>su-de</i>	3.2
Stroman, 1924b	<i>su-vl</i>	25
Mangelsdorf, 1926	<i>su-de₁</i>	38.5
Mangelsdorf, 1926	<i>su-de₈</i>	26.0
Mangelsdorf, 1926	<i>su-ge₁</i>	40.0

THE "B" GROUP, B , lg , sk , v_4 , ts_1

Investigator	Factors concerned	Crossing-over percentage
Emerson, 1920.....	ts_1-B	20.8
Emerson, 1920.....	ts_1-lg	45.8
Emerson, 1920.....	$B-lg$	29.2
Emerson, 1921 <i>b</i>	$B-lg$	30.5-33.4
Jones, 1925.....	$B-sk$	10.5
Demerec, 1924.....	$B-v_4$	16.8
Demerec, 1924.....	$lg-v_4$	43.2

THE "Y" GROUP, Y_1 , Pl , sm , w_1 , m_1 , m_2 , w_5 , w_6

Investigator	Factors concerned	Crossing-over percentage
Emerson, 1921 <i>b</i>	Y_1-Pl	24.2-30.0
Anderson, 1921.....	Y_1-Pl	29.7
Anderson, 1921.....	Y_1-sm	36.8
Anderson, 1921.....	$Pl-sm$	10.0
Stroman, 1924 <i>a</i>	$Pl-w_1$	25
Stroman, 1924 <i>a</i>	Y_1-m_1	33
Stroman, 1924 <i>a</i>	m_1-m_2	33
Lindstrom, 1924.....	Y_1-w_1	35
Stroman, 1924 <i>a</i>	Y_1-w_1	42
Demerec, 1923 <i>b</i>	Y_1-w_5	24.3
Demerec, 1923 <i>b</i>	Y_1-w_6	24.5
Demerec, 1923 <i>b</i>	w_5-w_6	36.9

THE "P" GROUP, br , P , ts_2 , f

Investigator	Factors concerned	Crossing-over percentage
Emerson, 1920.....	ts_2-P	none
Anderson and Emerson, 1923.....	ts_2-P	1.0
Anderson and Emerson, 1923.....	$P-f$	35
Kempton, 1921 <i>a</i>	$P-br$	35.5-38.1
Kempton, 1922.....	$ul-br$	16.8-30.0

THE "A" GROUP, $A-v_3$

Investigator	Factors concerned	Crossing-over percentage
Stroman, 1924 <i>a</i>	$A-v_3$	45
Demerec, 1924.....	$A-v_3$	independent

THE "Bn" GROUP, *Bn*, *ra*, *v₅*, *gl*, *pqa*, *Y_p*, *Y₂*

Investigator	Factors concerned	Crossing-over percentage
Kvakan, 1924	<i>Bn-gl</i>	18 7-29 4
Kvakan, 1924	<i>Bn-ra</i>	38 2
Kvakan, 1924	<i>Bn-v₅</i>	24 9
Kvakan, 1924	<i>gl-v₅</i>	6 2
Demerec, 1925	<i>Bn-pqa</i>	4 5
Hayes and Brewbaker, 1926	<i>Bn-Y_p</i>	20 5
Hayes and Brewbaker, 1926	<i>Bn-Y₂</i>	38 5

Besides these definite linkage groups, various other reports of linkage relations between certain factors have been made. For the most part these are not reported in sufficient detail or they have not been studied in relation to known groups so that it is definitely known whether they belong to any of the groups which have been differentiated.

Rather extensive tests have been made which indicate that probably these eight groups are independent of each other in inheritance. A brief summary of certain results will be made without making literature citations. Two or more factors of the *C* group have been found to be independent in inheritance of one or more members of the other seven groups. Factor *R* of the *R* group has been found to be independently inherited from one or more factors of other groups and several factors of the *R* group have been found to be independent in inheritance of factors in the *su* and *B* groups. Factors *su* and *Tu* in the *su* group have been found to be independent in inheritance of one or more factors in the *B*, *Y*, *P*, *A*, and *Bn* groups. Two or more factors of the *B* group are independent in inheritance of factors located in the *Y*, *P*, *A*, and *Bn* groups. Likewise, two or more factors of the *Y* group are independent of one or more factors located in the *P*, *A*, and *Bn* groups. Two factors of the *P* group are independent in inheritance of factors in the *A* and *Bn* groups, and both *A* and *v₃* are independent in inheritance of *Bn*. The group designated as *A* is perhaps not as definitely proved as the other seven groups, and the possibility is not precluded that groups which appear separate may be found to belong to the same linkage group when more interrelationships have been studied.

Variability of Crossing Over in Maize.—Emerson and Hutchison (1921), Eyster (1922a), and Stadler (1926) have compared the relative frequency of crossing over in microsporogenesis and megasporogenesis. In the studies the same *F₁* plants were used to compare the crossing-over percentages of male and female gametes. In some cases there were significant differences in crossing-over percentages. Stadler found that crossing-over percentages were significantly higher in male than in female gametes. Crossing-over percentages in male and female gametes

of the same plants were not found to be correlated. Crossing over in female gametes was apparently modified by age of plant or environmental conditions which had no effect upon the male gametes. He also found that there was a difference in unrelated families in crossing-over percentages in both male and female gametes.

Selective Fertilization.—In some cases there are slight significant deviations from an expected 3:1 ratio which leads to a deficiency of the recessive seeds. In studies of plants segregating for the waxy character, Brink and MacGillvray (1924) found that the pollen grains could be separated on the basis of their iodine reaction, the one giving the typical violet starch reaction and the other staining red. The proportion of waxy types was slightly in excess of the starchy, but there was a deficiency of waxy seeds in heterozygous ears. It was suggested that the slight chemical difference in the storage products of the pollen grains might cause a differential growth rate of pollen tubes.

Jones (1920) has observed selective fertilization in corn for its own pollen. Equal quantities of a plant's own pollen and of another type were mixed and applied to the plant. Characters were used whereby it was possible to separate self- and cross-pollinations from each other. Jones concluded that there was a "definite receptiveness of a plant for its own pollen and unlikeness instead of favoring fertilization is a hindrance." Selective fertilization was also studied in a sweet-pop cross (Jones, 1924b). It was concluded that there was an interaction between the pollen tube and the tissues in which it grows, such that pollen carrying the dominant or starchy factor is able to accomplish fertilization better in a sporophyte carrying the dominant factor in a homozygous or heterozygous condition than pollen carrying the recessive factor.

Inheritance of Other Endosperm Characters.—There are numerous other endosperm characters. Besides the four aleurone factors there is a factor for intensification of aleurone color (Fraser, 1924). Ordinarily red and purple aleurone carries this factor in the recessive condition. When the factor is in the dominant condition in the presence of *A*, *C*, and *R*, light red results and when *Pr* is present the color is light purple. Numerous other hereditary variations in aleurone color have been observed but not studied thoroughly.

Several investigators have described various types of hereditary defective seeds in maize which are simple recessives to normal types. Mangelsdorf (1926) has summarized many of these studies and for this reason no attempt will be made to refer to the various papers. Shrunken endosperm is the best known of these endosperm defects, as it has been extensively used in linkage studies. The number of types of hereditary defective seeds is apparently very large. Mangelsdorf has studied 14 defective types, each of which results from the homozygous recessive condition of a single factor pair. By means of intercrosses it was concluded that *de₂* and *de₁₁* were identical. Other combinations of 14 defectives were studied and the statement was made: "A sample of 14 types was taken at random from the grab bag which constitutes the germplasm of maize and 13 of these proved to be genetically distinct."

Mangelsdorf describes brittle endosperm which he found to be inherited as a simple recessive and which was intermediate in appearance between shrunken and sugary.

Types of premature germination were also worked with, which Eyster called "primitive sporophyte." Four genetically different simple recessives were studied. One case of duplicate factors was observed. These abnormal endosperm types well illustrate the enormous number of undesirable recessives in maize.

Colors in Plant Organs.—There is a group of anthocyanin color characters which are expressed in one or all of the following organs: cob, pericarp, silk, tassel, *i. e.*, glume, and in the leaves and stems. There are several different character expressions of a stable nature for this group of color characters. In some cases the color in two or more organs may be inherited as if due to a single factor. For example, the color in cob and pericarp is often correlated in inheritance. Emerson (1911) has found a case in which the factor for color in the cob behaves as an allelomorph of the factor for color in the pericarp. In the illustration given in the following table, R_1 represents the factor for cob color and R_2 the factor for pericarp color.

TABLE LX.—SUMMARY OF A CROSS IN WHICH A FACTOR FOR COB COLOR BEHAVED AS AN ALLELOMORPH OF A FACTOR FOR COLOR OF PERICARP

Parents			F_1			P_2	Appearance	
Zygote	Gametes	Appearance	Zygote	Gametes	Appearance	Zygotes	Cob	Pericarp
R_1R_1	R_1	Red in cob	R_1R_1	R_1 or R_2	Red (cob, red pericarp)	$1R_1R_1$	Red	White
R_2R_2	R_2	Red in pericarp				$2R_1R_1$ $1R_2R_2$	Red White	Red Red

East and Hayes (1911) have given a case of a cross between two reddish flush pericarp colors which developed only under light conditions, which gave a 15:1 ratio in F_2 . This indicates two separately inherited factors.

There are numerous expressions of colors. Hayes (1917) obtained four pericarp colors which bred comparatively true when self-fertilized. These were called solid red, in which the pericarp was uniformly red; variegated, in which the color was in deep red stripes of various sizes; pattern, in which the color was also in stripes but was much lighter in intensity; colorless, lacking color in the pericarp. The factors for red, variegated, pattern, and colorless appeared to form a series of multiple allelomorphs. The cross between pattern and variegated gave an increase in bud sports in F_1 , *i. e.*, ears which produce two sorts of pericarp color sharply differentiated; while in F_2 a few solid red ears were obtained and many striped ears. This was presented as an instance in heterozygous material in which a change in a character occurred. Without attempting an explanation it was pointed out that no such change occurred in six generations of selection in self-fertilized families of the red, striped, or pattern lines. Emerson (1914a, 1917) has studied the inheritance of these anthocyanin colors for several years. To explain the production of solid red in variegated races, he supposes a change or mutation in the factor V , for variegated, to S for self-color. Emerson concluded:

"These results favor the idea that single allelomorphic factors, rather than two or more closely linked factors, are responsible for the color pattern of both glumes and pericarp."

The concluding paragraph of Emerson's 1917 paper is directly in line with the ideas which have been developed throughout this book. With most plant-breeding material of farm crops, there is no evidence for basing a system of plant improvement upon mutations, as these are infrequent. With anthocyanin color characters of corn, inherited changes sometimes occur more frequently and such mutations become of selection value. This does not invalidate the pure-line conception for the large number of cases where factor stability is the rule. To quote from Emerson:

"The existence of the series of at least nine or ten multiple allelomorphs to which variegation belongs, indicates that a factor for pericarp color has mutated several times. Some of the factors for this series have not been observed to mutate, while others have mutated rarely and still others many times. In fact, the principal difference between certain of the factors is thought to lie in their relative frequencies of mutation."

Eyster (1924*l*, 1925) has made extensive studies of mosaic pericarp in maize and has suggested that the gene, for such characters as mosaic pericarp, is composed of gene elements which through structural rearrangement cause a change in the gene constitution.

Anderson (1924*a*) has presented a careful study of a series of cob and pericarp color crosses. The factors worked with were considered to belong to the *P* or pericarp series and might be written as *P^{rr}*, *P^{wr}*, which are factors, respectively, for red pericarp red cob and colorless pericarp red cob. In Anderson's study they are written as *RR* and *WR*. Anderson's purpose was to determine whether they were allelomorphic or whether linkage and crossing over occurred. If *WR* and *RW* were not allelomorphs then combination types would occur by crossing over and *WW* and *RR* could be obtained. That is, from a cross of red cob, white pericarp \times white cob, red pericarp, homozygous types which produce red cob, red pericarp and white cob, white pericarp could be obtained.

The following factors were studied:

Factors	Pericarp color	Cob color
<i>RR</i>	red	red
<i>OR</i>	light red to orange	red to orange
<i>WR</i>	white to pale orange	red
<i>OW</i>	light orange	white
<i>CW</i>	red or orange, white capped	white
<i>CR</i>	red or orange, white capped	red
<i>WW</i>	white	white
<i>VV</i>	variegated	variegated
<i>MO</i>	variegated, crown patch	light to white

There is considerable variation in each of these combinations. In general, color is more or less dominant over colorless. The tests for allelomorphicism were made by crossing two different types and out-crossing the *F*₁ to a *WW* type. The following crosses were made with results obtained:

CROSSES	EARS OBTAINED	
(<i>WR</i> \times <i>CW</i>) to <i>WW</i>	1751 <i>WR</i>	1684 <i>CW</i>
(<i>WR</i> \times <i>RR</i>) to <i>WW</i>	1001 <i>WR</i>	993 <i>RR</i> , 1 <i>VV</i>
(<i>CW</i> \times <i>RR</i>) to <i>WW</i>	1149 <i>CW</i>	1227 <i>RR</i>
(<i>WR</i> \times <i>VV</i>) to <i>WW</i>	2374 <i>WR</i>	2246 <i>VV</i> , 70 <i>RR</i> , 15 <i>WW</i>
(<i>OR</i> \times <i>VV</i>) to <i>WW</i>	773 <i>OR</i>	712 <i>VV</i> , 26 <i>RR</i> , 4 <i>WW</i>
(<i>CR</i> \times <i>VV</i>) to <i>WW</i> ¹	714 <i>CR</i>	683 <i>VV</i> , 14 <i>RR</i>
(<i>RR</i> \times <i>VV</i>) to <i>WW</i>	1399 <i>RR</i>	1308 <i>VV</i> , 2 <i>WW</i>
(<i>WR</i> \times <i>MO</i>) to <i>WW</i>	1509 <i>WR</i>	1508 <i>MO</i> , 3 <i>RR</i>
(<i>OR</i> \times <i>MO</i>) to <i>WW</i>	588 <i>OR</i>	551 <i>MO</i> , 1 <i>RR</i>
(<i>CW</i> \times <i>MO</i>) to <i>WW</i>	1663 <i>CW</i>	1572 <i>MO</i> , 5 <i>RR</i>
(<i>RR</i> \times <i>MO</i>) to <i>WW</i>	173 <i>RR</i>	174 <i>MO</i>

¹One combination type in *CR* \times *VV*, was obtained. In one other cross, *CW* \times *VV* which did not mature, one combination type ear was observed.

Most of the new types (different than the parents) occurred by mutation. "Two combination types appeared which may have been due to crossing over or more probably to stray pollination." The ears were frozen before maturity and their progeny could not be further tested.

The evidence is in favor of allelomorphism because

- 1 Tests have given no clear evidence of crossing over
- 2 In progenies of crosses of different pericarp types, parental types only have been observed to breed true
3. Inherited somatic mutation is more easily interpreted as resulting from modifications of single genes

There are two series of pericarp colors (Anderson and Emerson, 1923):

1. A series of allelomorphic or closely linked types which are characterized by a rather insoluble brick-red or an orange-red pigment. This is the series previously discussed and which Anderson concluded belonged to a series of multiple allelomorphs. The red series is the result of a combination of the factor *P* with the aleurone color factor *A*. The phenotypic conditions for pericarp colors in this series are as follows: *PA*, red; *Pa*, brown; *pA*, *pa*, colorless.

2. Cherry pericarp color, due to the presence in the pericarp of the water-soluble purple pigment (anthocyanin) found commonly in sheaths, leaves, anthers, etc. This pericarp color results from the interaction of the purple plant color factor *Pl*, the *A* aleurone factor, and the *r^h* allelomorph of the *R* aleurone factor series. The phenotypic conditions are *r^h Pl A*, cherry pericarp; *r^h Pl a*, *r^h pl A*, *r^h pl a*, colorless pericarp. Other allelomorphs of the *R* series give colorless pericarp only.

Studies of silk colors have been made by Anderson (1921) and four types have been differentiated:

Green: Silks green varying from a pale to yellowish green.

Red: Silks green, except when exposed to light when color may vary from a slight trace in the hairs to a dark-red color. The color underneath the husks is sometimes slightly reddish. Color due to the *R* factor

Salmon: Silks light orange to salmon. The color below the husks is the same as the exposed part of the silks.

Brown: Silks orange pink to pale brown. The color forms a series from almost green to salmon.

The salmon color is dependent on a recessive factor, *sm*, while brown is obtained in the presence of *A* when *sm* and *p* are recessive.

A Sm P, *A Sm p*, *a Sm P*, *a Sm p* = green
A sm P = salmon
A sm p = brown
a sm P, *a sm p* = green

The summary given here is quoted from Lundstrom's paper (1923b) and is taken from the work of Emerson on plant colors who has made extensive studies of these characters in maize.

PLANT	ANTHERS
" <i>A B Pl R^r</i> purple	purple
<i>A B^o Pl R^r</i> weak purple.	purple
<i>A B Pl R^o</i> purple	green
<i>A B pl R^r</i> sun red	pink
<i>A B^o pl R^r</i> weak sun red	pink
<i>A B pl R^o</i> sun red	green
<i>A b Pl R^r</i> dilute purple	purple
<i>A b Pl R^o</i> green	green

PLANT	ANTHERS
<i>A b pl R^r</i> dilute sun red.....	pink
<i>A b pl R^o</i> green.....	green
<i>a B Pl</i> brown.....	green
<i>a B pl</i> green (or slight brown in sheaths).....	green
<i>a b Pl</i> green (or slight brown in tassels).....	green
<i>a b Pl r^{ch}</i> green (considerable brown in tassel).....	green
<i>a b pl</i> green.....	green

"Factor r^r has the same effect on plant color as R^r , and r^o the same effect as R^o .

"When a purple plant that is heterozygous for the three fundamental factors *Aa Bb Pl pl* ($R^r R^r$ or $r^r r^r$) is self-fertilized, the following trihybrid ratio results:

- "27 *A B Pl*—purple stalk, leaves, and tassel; anthers purple
 9 *A B pl*—sun-red stalk, leaves, and tassel; anthers pink
 9 *a b Pl*—dilute purple leaves, and tassel; anthers purple
 3 *A b pl*—dilute sun-red leaves and tassel; anthers green
 9 *a B Pl*—brown stalk, leaves, and tassel; anthers green
 3 *a B pl*—green stalk, leaves, and tassel; anthers green
 3 *a b Pl*—green stalk, leaves, and tassel; anthers green
 1 *a b pl*—green stalk, leaves, and tassel; anthers green

"Striking confirmations of this hypothesis are evident when the dilute purple (showing surprisingly little purple color) type is crossed with the sun-red type (with no purple). The F_1 of this cross consists of full purple plants with a great amount of pigment. An identical F_1 results from a cross of the brown type \times the dilute sun red, neither parent showing any purple pigment whatsoever."

Dominant Plant Characters.—Perhaps the most striking is that characteristic of the pod group. Collins (1917) presented evidence proving that the ordinary type of tunicate or podded maize represents a case of imperfect dominance and is unfixable and related to the heterozygous condition. The homozygous, *Tu Tu*, type produces shorter ears than those of the other types and has sterile spikelets and very long pods and the glumes of the tassel are very long. No pollen is shed from such tassels. Seed may be produced in the pistillate flowers of the tassel through cross-pollination. In the ordinary podded-maize or heterozygous condition, *Tu tu*, each seed is enclosed in a short pod, otherwise the plant resembles normal maize. Another interesting type has been called Teopod by Lindstrom (1925b). It is a simple dominant character over normal corn. In this case a multiple dominant gene is responsible for many changes in morphological habit including changes in the pistillate and staminate inflorescences. It was called Teopod because of the resemblance to teosinte and pod corn.

Recessive Plant Characters.—The number of these is rather large. Several culm characters are of interest. In the type called adherent the leaves, bracts, and inflorescences adhere to one another in varying degrees. In some extreme cases the leaves of the young seedlings adhere. The firm union of upper leaves of more mature plants causes startling contortions. Adherence is probably a simple recessive (Kempton, 1921b). Zigzag can be noted only after the plant is nearly mature. Zigzag culm tends to dwarf the plant (Eyster, 1920, 1922b). It is probably a recessive and dependent upon the double recessive condition. Brachytic is characterized by great shortening of all internodes of the plant. It differs from the ordinary dwarf in that the size of the plant is not reduced except for the shortening of the internodes. (Kempton, 1920, 1921a.) It behaves as a simple recessive character. Dwarf and anther ear are types characterized by the production of stamens in the ear. Anther ear is a taller type of dwarf than the dwarf type. Each type is a simple recessive to normal and crosses of the two types give normals in F_1 . Dwarf anther ear, the double

recessive, is an extreme dwarf. The factors for these types are independently inherited (Emerson and Emerson, 1922).

Several leaf-character variations have been carefully studied. The type with the ligule and auricle absent is a simple recessive (Emerson, 1912*b*) and the factor for the character is located in the *B* group. Crinkled leaf, also described by Emerson (1921*a*), behaves as a simple recessive.

There are several tassel characters which are simple recessives. Two types called "tassel seed" are of interest as they belong to different linkage groups. Both are pistillate-flowered types. One originally called "tassel ear" is smaller and weaker than normal maize plants of the same line. The vigorous type, *ts*₂, belongs to the linkage group which also contains *br*, *P*, *f*. The smaller, weaker type is called *ts*₁ and belongs to the group *v*, *B*, *lg*.

The two most interesting ear characters which are simple recessives are ramose (Gernert, 1912) and silkless (Jones, 1925). With the ramose variation the normal pistillate ear is replaced by a compound structure resembling the staminate inflorescence. This character is linked with *Bn-v₅-gl*. Silkless, *sk*, produces normally vigorous tassels, few to no silks, rudimentary ovules, and, therefore, produces no seeds. It belongs to the group *ts*₁, *v*, *B*, *lg*.

Some Seed and Ear Characters.—Crosses between dents and flints were studied by East and Hayes (1911). There is no immediate visible effect of foreign pollen on the endosperm seed characters which separate these subspecies. Segregation occurred in *F*₂; some forms were obtained in *F*₃ which bred true to flint habit; some bred true to the dent type, while still others showed segregation. Two or more factors were necessary to explain results. The inheritance of the pointed condition of the seed which is characteristic of white rice pop was also studied by Hayes and East (1915). It was found possible to transfer this pointed condition to the dent subspecies. Results were complex and indicated that two or more cumulative factors were involved.

Size Characters.—Emerson and East (1913) summarized inheritance of size characters of seeds and ears. Weight of seed, seed measurement, number of rows, and length and diameter of ear were characters studied. In general, the *F*₁ condition was intermediate, and complex segregation occurred in *F*₂. The inheritance of height of plant, of period of maturity, and of suckering habit was also studied. The fact that a considerable series of fairly stable varieties is known which exhibit numerous conditions of the development of particular size characters, is also evidence of a complex inheritance. Segregation occurred in *F*₂ and extracted forms were obtained which approached the original parental conditions. Intermediates, as well as extremes, sometimes bred true.

Chemical Composition.—The classical selection experiments of the University of Illinois for the purpose of isolating high and low protein, and high and low oil strains, are well known. They prove conclusively that strains differing in chemical composition may be isolated by selection. Table LXI gives the results for 15 years' selection. This information was obtained through the kindness of Profs. L. H. Smith and C. M. Woodworth.

Progress during the latter years of the experiment has not been so rapid as during the early years, which is probably because the genetic limit for high and low protein and high and low oil production has nearly been obtained. These new strains have been named Illinois High Protein, Illinois Low Protein, Illinois High Oil, and Illinois Low Oil, respectively. The High and Low Protein strains were crossed with a normal Leaming variety by Hayes (1913*a*). The *F*₁ generation of the cross between Low Protein and Leaming produced approximately the same protein content as Illinois Low Protein, while the cross between Leaming and Illinois High Protein gave about the same protein content in *F*₁ as the normal Leaming variety. Results are given in Table LXII.

TABLE LXIB.—RESULT OF SELECTING MAIZE FOR HIGH AND FOR LOW OIL CONTENT, RESPECTIVELY

Average Percentage Oil in Crop Each Generation

Year	High strain	Average for period	Low strain	Average for period	Difference	Difference for period
1896	4 70		4 70			
1897	4 73		4 06		0 67	
1898	5 15		3 99		1 16	
1899	5 64		3 82		1 82	
1900	6 12	5 41	3.57	3 86	2 55	1 24
1901	6 09		3 43		2 66	
1902	6 41		3 02		3 39	
1903	6 50		2 97		3 53	
1904	6 97		2 89		4 08	
1905	7 29	6 65	2 58	2 98	4 71	3 67
1906	7 37		2 66		4 71	
1907	7 43		2 59		4 84	
1908	7 19		2 39		4 80	
1909	7 05		2 35		4.70	
1910	7 72	7 35	2 11	2 42	5 61	4 93
1911	7 51	..	2 05		5 46	
1912	7 70	.	2 18		5 52	
1913	8 15		1 90		6 25	
1914	8.29		1.98	...	6 31	
1915	8 46	8 02	2 07	2 03	6 30	5.99
1916	8.50		2 08	..	6 42	
1917	8 53		2.09	.	6 44	
1918	9 35	.	1 87	.	7 48	
1919	9 05		1.77	.	7 28	
1920	9 28	8.94	1 79	1 92	7 49	7.02
1921	9 94		1 70	.	8 24	
1922	9 86	.	1.67	.	8.19	
1923	10 08	..	1.58	.	8.50	
1924	9 86	..	1.51	..	8 35	
1925	10 21	9 99	1 43	1 58	8 78	8.41

TABLE LXII.—INHERITANCE OF PROTEIN IN THE FIRST-GENERATION CROSSES BETWEEN ILLINOIS LOW PROTEIN AND ILLINOIS HIGH PROTEIN AND STADT-MUELLER'S LEAMING

Variety	Number of ears analyzed	Variation in ears in protein content	Average protein content, dry basis
Illinois High Protein.....	19	11.95-17.10	14.87
Leaming, 1910 seed.....	13	7.75-16.28	11.85
<i>F</i> ₁ Cross.....	12	9.25-14.68	11.85
Illinois Low Protein.....	16	6.81-11.56	9.41
Leaming, 1911 seed.....	14	8.21-15.94	12.19
<i>F</i> ₁ Cross.....	9	7.69-11.86	9.18

Self-fertilization seems a logical means of obtaining pure races of different chemical compositions. Numerous ears should be self-fertilized and analyzed. Those that appear of promise may then be used and their breeding nature determined by the progeny test. As soon as homozygous

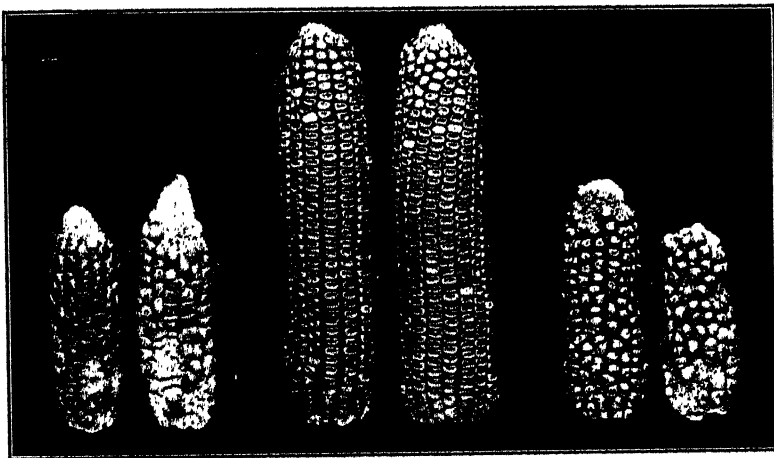


FIG. 49.—Two high protein strains of Minn. No. 13 at left and right respectively which have been self-fertilized for five years and first generation cross between them in the center. The *F*₁ yielded slightly more than normal Minn. No. 13 and analyzed 2½ per cent higher in protein content.

forms containing the desired characters have been isolated, they may be used as foundation stock for the production of an improved variety. That high-protein races may thus be isolated has been shown by Hayes and Garber (1919), East and Jones (1920), and Hayes (1922).

It was observed in the Minnesota studies that there was a correlation between the number of seeds produced by particular self-fertilized *F*₁ ears of the crosses A, B, and K, and protein content. Low number of seeds per ear was correlated with high

protein content. The F_1 crosses, A, B, and K, yielded slightly more than normal corn and gave 2.5 per cent higher protein content. It is no doubt true, as emphasized by East and Jones, that maximum yield of grain and high protein content probably cannot be obtained in the same variety.

TABLE LXIII.—PROTEIN CONTENT OF SELFED STRAINS OF MINNESOTA 13 AND CROSSES BETWEEN THEM

Strain No.	Average protein content		
	1916	1917	1918
1	15.82	14.03	15.10
4	14.47	13.06	14.93
Normal No. 13		10.17	10.25
1 × 4 F_1 Ear A			12.25
1 × 4 F_1 Ear B			12.44
1 × 4 F_1 Ear K			12.81

CHAPTER XVI

MAIZE BREEDING

A uniform technic has been developed for the breeder of self-fertilized small grain crops. Because of the self-pollination method of reproduction it is comparatively easy, by selection, to isolate homozygous lines which, if carefully handled, may be expected to remain relatively pure. Crosses between two or more varieties, for the purpose of combining within a single variety the desirable characters of the parents, have given favorable results. The obtaining of homozygous strains containing these desirable characters is a direct result of the application of Mendelian laws.

With cross-fertilized crops it is not so easy to control the male parentage and, for this reason, the improvement of this class of crops is more difficult. Mass selection, individual-plant selection without control of pollination, partial control of pollination by elimination of undesirable plants, partial space isolation, F_1 varietal crosses, and, more recently, the method of selection within self-fertilized lines and their recombination are some of the more important methods which have been used and are being used in corn breeding. A somewhat complete review of previous studies with literature citations was made by Richey (1922). Selection on the basis of ear characters has been a common practice of the farmer and experimental breeder.

Relation of Ear Characters to Yield.—Corn shows have accomplished much in teaching growers the characteristics of various standard varieties. They have, however, overemphasized the value of ear type as a means of corn improvement. Much work has been carried on with the view of determining the relation between various ear and plant characters and ability to give high yields. In general, no single character has been found to be so closely related with yielding ability as to be of much value from the standpoint of selection. Too close uniformity of type probably tends to reduce yield, for it has been learned that self-fertilization in corn causes a marked decrease in growth vigor as compared with cross-fertilization.

For the purpose of illustrating the general nature of results in this field, the work of Williams and Welton (1915) in Ohio may be used. They compared the yields of ears selected on the basis of wide differences of type. In the majority of cases selection was continuous, *i.e.*, long ears

from the long strain and short ears from the short strain. Summarized results are given in the following table:

TABLE LXIV.—RELATION BETWEEN EAR CHARACTERS AND YIELD

Characters worked with	Length of test, years	Differences in yield, bushels
Long <i>versus</i> short ears	10	Long 1 39
Cylindrical <i>versus</i> tapering	9	Tapering 1 65
Bare <i>versus</i> filled tips	8	Filled 0 34
Rough <i>versus</i> smooth dent	7	Smooth 1 76
High <i>versus</i> low shelling percentage	6	Low 0 42

These differences are very small considering that the yields obtained averaged between 60 and 70 bushels per acre. Although continuous selection isolated strains which differed considerably from each other, the yields were not markedly affected. The progressive change in shelling percentage of the progeny given in the following table, was most striking and illustrates how corn may be modified by selection.

TABLE LXV.—SHELLING PERCENTAGE AS AFFECTED BY CONTINUOUS SELECTION

Year	Shelling percentage in crop harvested	
	High	Low
1910	84 73	83.67
1911	87.30	84 66
1912	85 34	77 86
1913	87 09	76 93

The results presented in Table LXIV do not justify the belief that selection for ear type is a means of improving yield. Other experiments (Olson, *et al.*, 1918) have given results of a similar nature.

Richey and Willier (1925) made a statistical study by means of multiple correlation coefficients for the purpose of learning the possible relations between productiveness and some physical characteristics of the seed ears. It was concluded that from 2.5 to 6.7 per cent of the total variation in yielding ability in the ear-to-row plots was accounted for by the ear characters studied. Selection from among good seed ears on the basis of ear characters was not believed to be a desirable method of corn breeding. It was pointed out, however, that selecting longer, heavier

ears with relatively few rows and wide, thick kernels was desirable as a means of obtaining good seed for general planting.

Garrison and Richey (1925) made a study of the effects of continuous selection for ear type. Boone County White (C. I. 119) was used and selection made on the following basis:

- Strain No. 1—Rough ears, 8 inches or more long, with 20 or more rows of pinched-dented kernels.
- Strain No. 2—Rough ears, 8 inches or more long, with 16 rows of crease- to pinched-dented kernels.
- Strain No. 3—Smooth ears, 10 inches or more long, 20 or more rows of dimple- to slightly crease-dented kernels.
- Strain No. 4—Smooth ears, 10 inches or more long, with 14 rows of dimple-dented kernels.
- Strain No. 5—Smooth ears, 10 inches or more long, with 12 rows of dimple-dented kernels.
- Strain No. 6—Smooth ears, any length, with 8 rows of dimple-dented kernels. This strain originated from a few 8-rowed ears found among those in strains Nos. 4 and 5 in 1918.

Mixed seed from 50 or more ears was planted in a field or plot for each type of selection and continuous selection practiced for 8 years. The plots were isolated as much as possible and seed ears for the following year selected from interior rows only. Data were presented which proved that selection rapidly modified number of rows per ear.

The following statements are taken from *Bulletin* 1341 of the United States Department of Agriculture:

Without regard to the reason, it is evident that close selection to any type, as practiced in these experiments, resulted in decreased productiveness. The most productive strain, No. 4, the 14-rowed smooth selection, yielded 8.4 ± 0.20 per cent less than C. I. No. 119, and the least productive, No. 3, the 20-rowed smooth selection, 14.3 ± 0.19 per cent less. The 14-rowed smooth and 16-rowed rough selections, Nos. 4 and 2, were more productive and also departed less from the characteristic condition of the parent variety than the others.

In their practical application the experiments indicate that a decrease in vigor and productiveness similar to that following inbreeding may result from too close selection for a particular kind of ear. Careful experiments have failed to demonstrate a marked consistent superiority for any specific kind of ear. Other experiments have shown that the yields of crosses between varieties of corn frequently are more productive than the average of the parents, thus indicating that the parent varieties are too homozygous to permit maximum yields. Just what constitutes too close selection is not known. In view of the lack of evidence in favor of any particular kind of ear and the abundant evidence of the decreased yields that follow close breeding, however, it seems best to stay on the safe side by avoiding such close selection.

In view of the lack of evidence of marked consistent superiority for any particular kind of ear, it is unfortunate to teach that uniformity among the ears of a variety of corn is desirable by attaching importance to uniformity of sample, as is done in corn shows.

The studies of Hoffer, Holbert, and others have called attention to the stalk, ear, and root-rot diseases of corn. Certain investigators have shown that yield and freedom from disease are correlated. In other cases the so-called root-rot diseases were apparently of less importance. Winter (1925) has summarized several experiments and presents data to prove that "careful ear selection eliminates to some extent the necessity of a germination test."

Under certain conditions, selection of some particular ear character appears worth while. Thus Kiesselbach (1922) obtained some benefit from selection of long, slender, smooth-seed ears as compared with rough or with the original seed. It is doubtful, however, whether, under any circumstances, continued selection for any particular ear type is desirable. Selection in the field from vigorous healthy stalks appears a better procedure than ear selection and if long slender, smooth ears are desirable, field selection will lead to the production of this type.

Ear-to-row Breeding.—Corn is very largely cross-pollinated; therefore, selection under normal conditions considers only the mother plant. The ear-to-row method has been considered as the quickest means of isolating an improved variety. It was first introduced by Hopkins (1899) at the Illinois Experiment Station. As East (1908) pointed out, the method has some difficulties which have been partly obviated by improvements in technic. The improvements consisted of replication; *i.e.*, duplication of rows from the same ear in different parts of the field and of an attempt to overcome the harmful effects of too close inbreeding. The method outlined by Williams (1905, 1907) was to plant one-half the seed of each ear that was used for the ear-to-row test. The remnants of those ears which excelled by the progeny test were planted and the progeny intercrossed. Another feature of Williams' plan was to influence several breeders to work with the same variety. New blood was then introduced into the ear-to-row plot of each breeder every fourth or fifth year from a grower who was using the same breeding method. The difficulties of the method are that a yearly plot is needed for the ear-to-row test, an isolated plot for the crossing of the remnants, a multiplication or seed plot, and the general field. Montgomery (1909) suggested a plan which obviates some of these difficulties. This plan is to grow an ear-to-row plot only once in several years, and in the intervening years use a bulk seed plot planted by the hill method, selecting only from the vigorous stalks in perfect stand hills (see Chap. XXI). A review of the literature on ear-to-row breeding seems unnecessary. It seems sufficient here to point out that there are no experiments which show conclusively that continued ear-to-row breeding may be expected to give a significantly higher yield than seed produced by the seed-plot method. Ear-to-row breeding with a variety that has not been systematically selected is doubtless the most rapid means available to the corn farmer for the

isolation of better yielding hereditary combinations. As an illustration of the sort of results usually obtained, the results of a 5 years' study as carried on at Nebraska Station (Kiesselbach, 1916) are given in the following table:

TABLE LXVI.—EFFECT OF EAR-TO-ROW BREEDING ON THE YIELD OF HOGUE'S YELLOW DENT, AT THE NEBRASKA STATION, 1911-1915

Description	Yield in bushels per acre					
	1911	1912	1913	1914	1915	Average
Original Hogue's Yellow Dent.....	42.6	51.6	9.8	62.8	79.5	49.3
Continuous ear-to-row selection.....	44.0	52.9	7.7	65.3	76.8	49.3
Increase from single ear-to-row strain.	38.2	45.6	7.3	55.0	75.3	44.3
Increase from composite four ear-to-row strains.....	42.5	54.6	12.1	63.5	80.0	50.5

These studies with Hogue's Yellow Dent were started in 1902. This variety was selected because of its yielding ability as shown by varietal test. Apparently, no method of selection has given very strikingly beneficial results.

Studies of methods of selection with Rustler White Dent (Hayes and Alexander, 1924) were carried on in Minnesota. This variety was chosen for the study as it showed considerable deviation in ear type and as it had not been selected previously by the ear-to-row method. It had the advantage of being adapted to the climatic conditions of central Minnesota, which was necessary as the problem was planned as a means of learning how best to select seed of an adapted variety.

The methods used in the Rustler selection test were as follows: as far as possible, the field in which each method of selection was carried on was separated from other fields of corn. The selection was continuous from year to year. The selected seed, for the different methods, was stored in a comparable way, except as noted later, and only seed from ears which showed high germination ability by actual trial was used for planting. The comparable-yield trials for the different methods of selection were made on the same field. Three-row plots, each row approximately 36 hills long, were used. The central row was used for the yield comparison. Three systematically distributed plots were used for the yield comparison except in 1920 when four plots were used. The methods of selection were as follows:

1. Selection of good ears at husking. Three seeds were planted in each hill and the corn was cut and shocked when mature. Later in the fall the better-looking ears were thrown into a pile when the corn was

husked and reserved for seed. This method was isolated from other cornfields.

2 Selection during seed-corn week¹ from perfect stand hills and vigorous stalks. Only well-matured ears were chosen but no close selection to ear type was made. The ears were stored immediately in a well-ventilated room, each ear having individual space for proper curing. The lower series on field X was used each year and similarly selected seed was used to plant the adjacent series on which silage corn was grown. This method was isolated from other methods.

3. As in method 2, except that the selected stalks were shocked and the ears husked later in the fall.

4. Selected as in method 3 in the field during seed-corn week. After husking, the ears were carefully examined for ear type. Only ears of high score-card type were used for planting the following year. Selection was made for good butts, medium denting, straight rows, cylindrical ear, 14- to 16-rowed ears, and good ear length. Field C, the manured half-acre, was used for this method through cooperation with the farm-crops section. Some cross-pollination may have occurred between the plants on this field and those in the ear-to-row plot, although the fields were a considerable distance apart.

5. This is called "Montgomery's method" because the plan was suggested originally by Montgomery. It consists of an ear-to-row test the first year, followed by a mixture of seed of the remnants of the 25 better yielding ears as determined by the ear-to-row test. Approximately 100 ears were used for the original ear-to-row selection. In subsequent years the method pursued was similar to method 3. By selecting from that part of the field which was the farthest from the ear-to-row plot, the isolation was fairly good.

6. Williams' method. The purpose of this plan is to isolate high-yielding ears by the ear-to-row plan, cross the remnants of the three highest-yielding ears the following year, and multiply the crosses in a seed plot the following year. The seed plot is considered the place to produce commercial seed. The ear to-row, the crossing, and the multiplying plots are used each year. The crossing and multiplication plots were well isolated from other cornfields.

From Williams' plan two sorts of seed have been used for the yield trials: (1) F_1 crossed seed produced by crossing the remnants of the three higher-yielding ears, (2) increase plot seed obtained by planting F_1 crossed seed. Field T was used for this increase through cooperation with the farm-crops section.

Yield trials were made by the use of replicated plots. Results are presented in the following table:

¹ The period set by the Agricultural Extension Division for selection of seed under field conditions.

TABLE LXVII.—METHOD OF SELECTION OF SEED OF RUSTLER DENT CORN IN RELATION TO YIELD

Method of selection	Yield in bushels per acre				
	1920	1921	1922	1923	Average
1. At husking.....	50.2 ± 1.6	64.1 ± 1.3	48.9 ± 1.3	54.9 ± 1.9	54.5 ± 0.8
2. Perfect stand hills for yield, seed stored immediately..	47.9 ± 1.5	64.1 ± 1.3	49.2 ± 1.3	56.5 ± 1.9	54.4 ± 0.8
3. Perfect stand hills for yield, seed cured in shock.....	48.1 ± 1.5	63.7 ± 1.3	48.9 ± 1.3	56.5 ± 1.9	54.3 ± 0.8
4. As in method 3 in field, selection later for score- card type.....	46.6 ± 1.4	63.7 ± 1.3	47.2 ± 1.2	55.1 ± 1.9	53.2 ± 0.7
5. Montgomery's method.....	49.5 ± 1.5	66.0 ± 1.3	49.5 ± 1.3	55.9 ± 1.9	55.2 ± 0.8
6. Williams' method, P_1 crossed seed.....	47.0 ± 1.4	65.7 ± 1.3	49.1 ± 1.3	60.3 ± 2.1	55.5 ± 0.8
7. Williams' method, increase plot.....		60.9 ± 1.2	48.2 ± 1.2	52.3 ± 1.8	

The differences are not very great although selection for score-card type of ear appeared to cause a slight reduction in yielding ability. By the "Student" method the chances are 37:1 that this reduction is significant.

Smith and Brunson (1925), at Illinois, have studied the value of practical methods of corn breeding. In the studies of ear-to-row breeding, special precautions were taken to overcome the harmful effects of inbreeding. The conclusion is reached that mass selection was the most effective simple method of selecting corn for yield and that ear-to-row breeding cannot be recommended as a means of increasing the yielding ability of a well-adapted variety.

Home-grown Seed.—The value of using home-grown seed of a variety which has shown its yielding ability by competitive test is well known to most corn growers. Nebraska results may again be used for illustrative purposes.

TABLE LXVIII.—EFFECT OF ACCLIMATIZATION ON CORN

Character of seed	Yield in bushels per acre
Show corn from Illinois, Indiana, and Ohio (5 varieties).....	39.8
Seed from growers in state (5 varieties).....	45.6
Local varieties near experiment station (7 varieties).....	48.8

The data presented in Table LXVIII show that home-grown seed usually yields better than seed brought from a distance. A system of broad breeding, the use of a high-yielding, adapted variety, and the storage of the seed so that it will germinate vigorously are important practices which should be a part of each corn-breeder's plan.



FIG 50.—Munn. No. 13 self-fertilized high protein strain No. 1. This strain has dark green leaves, medium sized ears, and the tassels are somewhat scantily provided with pollen

Immediate Effect of Crossing on Size of Seed.—The question of immediate effect of crossing on size of seed has received considerable attention, and Carrier (1919) has considered this a main cause for the conflicting results of corn experiments. He demonstrated the fact that mixtures of seed of different strains gave higher yields than seed of a single strain and explained the results on the basis of increased yield due to the increased weight of the endosperm of varietal crosses as compared with normally pollinated seeds within a variety.

Other investigations have partially supported Carrier's contentions. Studies of the effect of pollen of a different strain or variety on endosperm development are given in the following table:

TABLE LXIX.—IMMEDIATE EFFECT OF POLLINATION ON ENDOSPERM WEIGHT

Number of tests	Number in which weight of crossed seed exceeds that of normal seed	Number in which weight of normal seed exceeds that of crossed seed	Average percentage of increase due to immediate effect of foreign pollination	Authority	Method
5	5	0	8.8	Collins and Kempton, 1913	Mixture of pollen of same and different variety Mixture of pollen of same and different variety Selfed strains and crosses between them Plants of ordinary varieties Selfed strains and crosses
31	23	8	2.8	Wolf, 1915	
2	2	0	19.2	Jones, 1918	
7	4	3	0.22	Kiesselbach, 1922	
4	4	0	11.2	Kiesselbach, 1922	

These results show that there was an immediate effect of pollen on the weight of the endosperm of crossed seed compared with that produced by intravarietal pollination. In varietal tests, however, as conducted by the plot method, the degree of crossing between different varieties would not usually be over 50 per cent. Averaging the results of Wolf and of Collins and Kempton gives about 5 per cent increase due to crossing. Reducing this by one-half gives an error in varietal tests of not more than 2.5 per cent as a result of increased endosperm development due to the immediate effect of foreign pollen. As the studies of Collins and Kempton were made with widely different varieties, the results are probably somewhat more striking than if more closely related forms had been used.

Kiesselbach (1922) observed only slight increases in weight of hybrid seeds of normal varieties. The differences obtained by various investigators apparently are correlated with the differences in the degree of heterozygosity of the varieties with which they worked.

F₁ Varietal Crosses.—The utilization of hybrids as a means of obtaining more vigorous types was urged by Beal (1876-1882). Since then there has been frequent mention of the vigor of *F*₁ crosses, and Morrow and Gardner (1893, 1894) outlined a plan for the production of crossed corn seed. Renewed interest in this subject was aroused as a result of the publications of East (1908b) and Shull (1908, 1909) on the effects of inbreeding and cross-breeding, and of Collins (1909, 1910) on the value of

first generation hybrids in corn. Many experiments in which first generation crosses have been compared with their parents have been made. In Table LXX only those varietal crosses are used in which the F_1 has been compared with both parents.

Some of the increases from these varietal crosses are very marked. In other cases the F_1 varietal hybrid is no more vigorous than the normal varieties.

Similar crosses, as reported by Hayes and Olson (1919), were studied for the succeeding 5-year period, 1919 to 1923 (Hayes and Alexander, 1924). During this latter period Minnesota 13, the male parent, was



FIG. 51.—Minn. No. 13 high protein strain No. 4. Short, erect strain with light green leaves. Produces good ears. Tassels are plentifully supplied with pollen.

selected on the basis of vigorous stalks in perfect-stand hills without selection for ear type. Prior to this period this strain of Minnesota 13 had been closely selected for ear type. On the average, the F_1 crosses during the last 5-year period yielded about the same as the average of the parents although certain crosses of an early flint and Minnesota 13 yielded as much as Minnesota 13 and matured earlier.

Except for some special condition, it appears that F_1 varietal crosses are of no material value as a means of increasing yielding ability, provided a broad method of breeding is used by the corn breeder without too close selection to type.

Recent Methods of Corn Breeding.—The development of the practice of breeding cross-pollinated plants by some method of controlled pollina-

TABLE LXX.—FIRST-GENERATION CROSSES BETWEEN CORN VARIETIES

Authority	Location	A	B	C	D	E	F	G	Method of test and remarks
Hartley, <i>et al.</i> , 1912.....	Chico, Cal.	16	4	12	- 2.5	13	3	+ 7.7	Single row plots. Female parents unadapted, males adapted.
Hayes and East, 1911.....	Mt. Carmel, Conn.	3	2	1	+ 1.5	3	3	+28.0	Male parents adapted, females unadapted.
Collins, 1910a.....	Lanham, Md.	16	12	4	+16.6	14	2	+38.0	Widely different types. Single plot of 16 hills.
Collins, 1910b.....	Washington, D. C.	10	7	3	+25.6	8	2	+81.0	Sweet corn. Single plots.
Morrow and Gardner, 1892.....	Champaign, Ill.	5	3	2	+ 7.0	5	0	+14.0	Adapted varieties. Single plot tests.
Morrow and Gardner, 1893.....	Champaign, Ill.	4	2	2	- 1.2	3	1	+ 7.7	Adapted varieties. Single plot tests.
Hayes, 1913a.....	Mt. Carmel, Conn., 1912	19	10	9	- 3.5	16	3	+10.1	Adapted varieties, one replication, single row plots.
Hayes, 1913a.....	Mt. Carmel, Conn., 1913	8	5	3	+ 5.3	5	3	+ 8.3	Adapted varieties. One plot of three rows each.
Hartley, <i>et al.</i> , 1912.....	Sherman, Waco, Corsicana, Tex.	11	4	7	- 0.1	10	1	+ 9.5	Adapted varieties. Single row plot. Average of test in three localities.
Belling, 1912b.....	Florida	1	1	..	+43.7	+48.0	Adapted varieties. Single plot tests.
Williams and Welton, 1915.....	Ohio	7	5	2	+ 0.3	7	6	+ 3.2	Adapted varieties. Single plot tests.
Jones, <i>et al.</i> , 1917.....	Mt. Carmel and Storrs, Conn.	17	9	8	- 0.2	14	3	+ 6.2	Adapted varieties. Single plot tests. Average of two localities.
Jones, <i>et al.</i> , 1917.....	Mt. Carmel, Conn.	12	9	2	+ 4.2	11	1	+16.3	Adapted varieties. Single plot tests.
Hutchison and Wolf, 1917.....	Blacksburg, Va.	4	1	3	-11.2	3	1	+ 4.3	Adapted varieties. Four-row plots. Two replications.
Kieselbach, 1918.....	Lincoln, Neb.	10	- 1.9	Adapted varieties. All late varieties.
Kieselbach, 1916.....	Lincoln, Neb.	3	+ 1.2	Adapted varieties. Crosses between early and late varieties.
Hayes and Olson, 1919.....	Univ. Farm, St. Paul, Minn.	11	10	1	+11.7	10	1	+14.5	Adapted varieties. One replication, three-row plots. Average results of two to four years.

A. Number of crosses tested.

B. Number of crosses yielding more than better parent.

C. Number of crosses yielding less than better parent.

D. Average percentage increase or decrease as compared with better parent.

E. Number of crosses exceeding yield of average of parents.

F. Number of crosses yielding less than average of parents.

G. Average percentage increase or decrease as compared with average of parents.

tion has been a gradual one. The method originated as a result of intensive studies of the effects of self-fertilization in cross-pollinated species and throughout this study the work with corn has been of fundamental importance. The studies which were initiated over 15 years ago by Dr. E. M. East at the Connecticut Station by Dr. G. H. Shull at Cold Spring Harbor, by various workers of the Bureau of Plant Industry, and others, had as their aim the development of a more intensive knowledge of the physiology of inheritance of the corn plant, with the belief that such studies were essential to the development of better methods of breeding. In 1910 Dr. Shull emphasized the value of isolating pure lines and of using F_1 crosses between pure lines for maximum production. He makes the significant comment: "I feel quite sure that the results of such investigations will lead to some hybridization method in the breeding of this crop."

The purpose of the newer methods is to enable the breeder to control the factors of inheritance. A brief summary of the main steps is given here. Numerous plants of a desirable adapted commercial variety are self-pollinated. This is accomplished by covering the ear with a paper bag before the silks appear. The tassel is covered with a separate bag and after the silks are well out the pollen is poured from the tassel bag over the silk. The ear is protected from foreign pollen by again covering the ear shoot with the bag. The seed for each subsequent generation is obtained by self-pollinating plants which seem desirable. Such self-fertilized lines rapidly become uniform and remain so as long as self-fertilization is continued. By the method used, undesirable germ plasm is eliminated and desirable germ plasm made known. No selfed strains have been obtained which are as vigorous as normal varieties. Selfed strains differ widely from each other. Some of the more important differences are:

1. Resistance or susceptibility to ear, stalk, and root rots and to smut.¹
2. Height of plant, length, shape of ear, and ear production per plant.
3. Size of seed.
4. Strength of stalk and non-lodging ability.
5. The number and sort of striking abnormalities present.

This method allows the breeder to discard strains which are highly inferior. The best-appearing strains which approach homozygosity are selected for further breeding operations. These can be selected after the strains have been selfed for four or more generations.

There are various questions regarding methods of work which are unanswered. It is generally recognized that the importance of obtaining the best possible selfed lines warrants extensive studies. Whether or not larger numbers of original selfed lines should be used or smaller numbers with more extensive selection within each line is not yet known. It also

¹ See Jones, 1918; Holbert and others, 1924, Garber and Quisenberry, 1925; Hayes and others, 1924; and Immer and Christensen, 1926.

appears probable that better selfed lines can be obtained by crosses of existing lines or from the better F_1 hybrids of selfed lines with the view of combining within a single line the desirable characters of two or more lines (see Jones and Mangelsdorf, 1925; Kyle and Stoneberg, 1925; Hayes, 1926; Richey and Mayer, 1925). After obtaining selfed lines the more promising are used in making F_1 crosses or in developing improved varieties. Three general methods of using selfed lines are being tried out.



FIG. 52.— F_1 cross of Minn. self-fertilized strains No. 1 \times No. 4.

These are: (1) single crosses, (2) double crosses, and (3) synthetic recombination of several selfed strains.

In the single-cross plan, two selfed strains are crossed and the F_1 grown as the commercial crop. Certain difficulties are involved in this. The low yield of seed which is usually obtained from closely inbred lines will result in increased cost of seed production. In many inbred lines the size of seed is smaller than that of the commercial variety from which the inbred line was obtained. This results in some handicap for the young plant when single crosses are used for the commercial crop. With the

production of better selfed strains, it is possible that single crosses may prove more feasible.

The double-cross plan, outlined by Jones (1920), overcomes some of these difficulties, although, instead of making one cross to obtain commercial seed, three crosses must be made. A double cross is a first-generation cross between two single crosses. Four selfed strains which combine well together are used. The double-cross plan has the advantage that vigorous F_1 crosses are used as parents. The variability of the individual plants of a double cross will be greater than in a single cross. This will result in a prolonged period of pollination which, under certain environmental conditions, is an advantage.

If either the single- or double-cross plan is used, F_1 seed must be produced each year, as the selection of seed from F_1 crosses leads to marked reductions in yielding ability in later generations.

The production of improved varieties synthetically, by a cross of several selfed lines and subsequent selection, aims at the improvement of the variety without the necessity of making an F_1 cross each year. It appears probable, however, that it will be very difficult to obtain a variety which will be as vigorous as certain F_1 crosses. When a single character, such as disease resistance, is of outstanding importance, the plan appears a very desirable one.

There is also the possibility that F_1 crosses of synthetic varieties can be used, providing the F_1 cross proves to be the general method which is adopted for seed production.

Single and Double Crosses of Selfed Lines.—A double cross, known as Burr-Leaming, has received wide publicity because of its yielding ability. This double cross was compared by Jones with the five highest-yielding varieties which were obtained after extensive studies of corn varieties in Connecticut (Table LXXI). The average increase in bushels of ear corn of the Burr-Leaming over the average of the five varieties was 27.1 per cent for a 5-year period.

TABLE LXXI.—A COMPARISON OF THE YIELDS IN BUSHEL PER ACRE OBTAINED FROM THE DOUBLE-CROSS BURR-LEAMING, WITH THE AVERAGE YIELDS OBTAINED FROM THE FIVE HIGHEST-YIELDING VARIETIES (Connecticut Station, after Jones)

Varieties compared	Year grown					Average
	1918 bushels	1919 bushels	1920 bushels	1921 bushels	1922 bushels	
Double-cross Burr-Leaming	116	88	55	95	63	83.4
Average of five highest-yielding varieties	82	64	47	81	54	65.6
Average increase, 27.1						

Extensive studies are now under way at Connecticut Station in which selfed lines from the better Connecticut varieties are being used. One double cross, studied in 1924 by Jones, indicates that large increases in yields may be expected (Table LXXII).

In this case, an F_1 cross of two inbred Century Dent strains was crossed reciprocally with an F_1 of two Leaming strains and the yields of the double crosses were compared with those obtained from Century Dent and Leaming. These studies are of interest, for Century Dent and Leaming are two of the best Connecticut varieties. The double cross, Century $F_1 \times$ Leaming F_1 , exceeded the higher-yielding variety by 21.6 per cent and the reciprocal yielded 37.4 per cent more than the higher-yielding variety.

TABLE LXXII.—A COMPARISON OF THE YIELDS IN BUSHEL PER ACRE FROM CENTURY DENT, BEARDSLEY'S LEAMING, AND A DOUBLE CROSS OBTAINED FROM TWO INBRED STRAINS OF CENTURY DENT BY TWO INBRED STRAINS OF LEAMING
(Connecticut Station, after Jones' 1924 results)

Variety or cross	Plot 1, bushels	Plot 2, bushels	Average, bushels	Percentage yield, Century as 100
Century.....	46.6	50.6	48.6	100.0
Leaming.....	36.1	51.1	43.6	89.7
Century $F_1 \times$ Leaming F_1	63.1	70.6	66.8	137.4
Leaming $F_1 \times$ Century F_1	51.1	67.1	59.1	121.6

Several years ago, Richey reported the production of a high-yielding F_1 hybrid of Whatley \times St. Charles White which appeared superior to any commercial variety grown in the region in which the study was made. Selfed lines were isolated from the F_2 generation and selections made within these lines for 6 years. Crosses between these selfed lines were grown at Knoxville, Tenn., in 1922 and 1923. The studies were made by the hill-check plan. Certain crosses were of much promise, while others were of little value. This brings out the fact, recognized by most investigators of modern methods of corn breeding, that the present-day methods are primarily those of controlled selection. The combination of selfed lines which together contain the greatest number of favorable growth factors is the ultimate aim. Three of the better-producing crosses reported by Richey and Mayer averaged 30 per cent higher in yield than the parent variety.

Extensive studies are being carried on in Nebraska by Kiessclbach (1922). The results of a 4-year trial of several single crosses in comparison with the original variety have been reported (Table LXXIII). The highest-yielding cross produced 53.2 bushels as an average for the 4 years, while the original variety averaged 41.2 bushels. This cross exceeded

the yield of the original variety each of the 4 years, although in 1 year the difference was well within the limits of experimental error. The eight crosses for which data are presented exceeded the original variety in bushels of shelled corn by an average of 17.2 per cent. In Nebraska, selfed strains with low leaf area yielded more than strains with high leaf area and crosses between strains with low leaf area were the most promising.

TABLE LXXIII.—COMPARISON OF YIELDS IN BUSHELS PER ACRE OF F_1 CROSSES BETWEEN SELFED STRAINS WITH THE ORIGINAL VARIETY FROM WHICH THE SELFED LINES WERE OBTAINED (*Nebraska Station, after Kresselbach, 1922*)

Cross or variety	Bushels per acre of shelled corn				Average
	1913	1915	1916	1917	
4 × 12	22 0	61 9	38 8	60 6	45 8
4 × 1	26 8	64 8	53 2	41 6	46 6
12 × 5	22 8	69 5	44 6	48 5	46 4
8 × 2	20 1	71 3	66 2	51 9	52 4
12 × 2	21 9	73 6	58 0	59 4	53 2
10 × 12	22 7	57 9	51 5	53 6	46 4
10 × 5	21 2	61 0	43 3	51 0	44 9
Average..	23 3	66 9	51 7	59 3	48 3
Original . .	11 4	73 1	34 5	46 0	41 2

Results of corn-yield contests conducted by the Iowa Corn and Small Grain Growers' Association in 1924 have aided materially in proving the high-yielding ability of certain crosses. The data here summarized were taken from the report of the 1924 tests. H. A. Wallace, an enthusiastic supporter of the modern methods of corn breeding, has furnished data regarding these contests and other studies which he is conducting. The results of the contest in 1924 for the South Central Section, where several crosses were entered, are summarized in the following table:

TABLE LXXIV.—YIELDS IN BUSHELS PER ACRE OF WINNERS AND SOURCE OF SEED IN 1924 (*Data from Iowa Corn-yield Contests, summarized by Wallace*)

Cross or variety	Place taken	Yield in bushels
Cross of inbred strains, U. S. D. A	First	51 3
Cross of inbred strains of Wallace...	Second	45 1
A cross of two strains of Leaning...	Third	41.2
Leaning 1-6 × Illinois Low Protein...	Fourth	40 3
Chinese Bloody Butcher inbred strain × Illinois Low Protein	Fifth	40.2
Commercial Reid's Yellow, Highest yielder...	39.1
Average yield of four crosses, inbred strains involved...	44.2
Reid's Yellow Dent, average yield of 34 strains	34.5

The five highest-yielding sorts were F_1 crosses and, in four cases, an inbred strain was used as one or both of the parents. The highest yield, 51.3 bushels per acre, was obtained from a cross entered by the United States Department of Agriculture, while the highest-yielding commercial variety, a strain of Reid's Yellow Dent, produced 39.1 bushels per acre. The average yield of four crosses in which inbred strains were involved was 44.2 bushels, while the average yield of the 34 strains of Reid's Yellow Dent entered in the contest was 34.5 bushels. Mr. Wallace is conducting extensive tests at Ames in cooperation with H. D. Hughes and reports that many of these crosses have yielded much more than the standard variety with which they have been compared.

Professor Hughes¹ made the following statement in a recent letter:

From the results secured thus far, it is entirely evident that decidedly better yields can be secured from hybridizing pure lines than can be had from the best standard varieties of which we know. The data would also indicate that extensive ear-row breeding with subsequent crossing of the best lines even when carried through a long period of years cannot be expected to give the results to be had from the production of pure lines and the use of F_1 seed.

Crosses in which selfed strains were used have been grown at University Farm, St. Paul, Minn., for several years. Rather extensive field-plot trials of double crosses were made in 1924 and 1925. During these two seasons the selfed lines used were isolated previously from standard high-yielding Minnesota varieties. Two such varieties recognized as standard for central Minnesota (Minn. 13) and Rustler White Dent, have been grown at University Farm for many years, the seed being selected in the field from perfect-stand hills and from vigorous healthy stalks. Close selection to score-card type of ear has not been practiced in recent years. Seed for three other varieties has been purchased yearly from Northrup King Seed Company and represents the better selections for these varieties.

The selfed strains used for the crosses were picked out on the basis of yield and the absence of striking abnormalities. Each F_1 cross was made by crossing two selfed strains within a variety which appeared unlike each other and the double crosses of these F_1 crosses were made at random. It is recognized that it would be more desirable to determine the strains which would combine to produce the better-yielding crosses; this method is being tried out. In the meantime, however, it appeared of interest to see what the results would be from combining on the basis of observable characters alone. The results for the two crop seasons are presented in Table LXXV.

In 1924, of a total of 21 double crosses tested, 3 yielded less than the higher-yielding commercial variety. One double cross exceeded the

¹ Letter of Nov. 12, 1925, from Professor Hughes to the writer.

better commercial variety by 30 per cent. The seven double crosses, in which dent inbred strains were used, yielded 13 per cent more on the average than the better variety, while 12 flint-dent crosses averaged 9 per cent more than the better variety. Of two flint double crosses one gave a low yield and the other yielded rather well. The results in 1925 were similar and certainly indicate that double crosses in which desirable-appearing selfed lines are used may be expected to yield more than the present standard varieties.

TABLE LXXV—PERCENTAGE YIELD OF DOUBLE CROSSES OBTAINED BY CROSSING F_1 CROSSES BETWEEN SELFED LINES WHERE 100 IS TAKEN AS THE YIELD OF THE HIGHER-YIELDING STANDARD VARIETY (*University Farm, St. Paul, Minn., 1924-1925*)

Crosses, 1924	Percentage yield classes										Number of crosses	Average percentage yield
	70	95	100	105	110	115	120	125	130			
Dent crosses		1	2	1	1	.	1	1	7	113 3	
Flint-dent crosses.....	2	.		3	2	3	1	1	.	12	109 4	
Flint crosses	1		.		.		1	.	.	2	95 5	

Crosses, 1925	Percentage yield classes										Number of crosses	Average percentage yield
	85	90	95	100	105	110	115	120	125	130		
Dent crosses....		.	1	2	1	1	1	2	..	1	9	110.1
Flint-dent crosses.		1	1	.	1	3	107 3
Flint crosses...	1	..	1	2	1	5	105 5

Synthetic Combination of Several Selfed Lines.—The production of improved varieties through the recombination of several selfed strains has one advantage over either the single- or double-cross plan in that the farmer can save his own seed from the yearly crop and that yearly crosses need not be made. Little data regarding the value of this method are available.

At University Farm several recombinations of selfed strains within a variety were made in 1923 and the F_2 recombinations were compared with commercial varieties in 1925.

The methods used were as follows: Selfed strains were selected which appeared superior to the average and which were free from striking abnormalities. The recombination of selfed strains was obtained by pollinating several plants of each strain of a variety with a mixture of pollen from other strains of the same variety. An equal number of seeds from each such cross of each strain was bulked and planted the following

year. Seed for later generations within each recombination was obtained by pollinating 50 plants with a mixture of pollen of 50 other plants. The same results could be obtained by mixing seed of all selfed strains to be used and by planting them in an isolated plot. Several years would be necessary to obtain thorough recombination. The comparisons of yielding ability of the standard varieties and of the F_2 recombinations are given in the following table. According to genetic theory, yields in later segregating generations should be as good as in F_2 .

TABLE LXXVI.—YIELD OF SYNTHETIC VARIETIES COMPARED WITH COMMERCIAL VARIETIES (*University Farm, St. Paul, Minn., 1925*)

Variety	Strains used for recombination		Yield bushels per acre	Per cent increase or decrease
	Years selfed	Number		
Minn. 13.....	51.3	
Minn. 13 F_2 recombination.....	1	5	45.3	- 11.7
	3	3		
	8	1		
Rustler.....	44.8	
Rustler F_2 recombination.....	1	2	47.5	+ 6.0
	2	7		
	3	5		
	4	3		
Northwestern Dent.....	51.9	
Northwestern Dent F_2 recombination	1	2	60.5	+ 16.6
	3	8		
King Phillip.....	40.3	
King Phillip F_2 recombination.....	3	11	43.3	+ 7.4
Longfellow.....	43.9	
Longfellow F_2 recombination.....	3	8	40.1	- 8.7

For the five comparisons there were three F_2 recombination families which yielded more than the standard variety and two which yielded less. The Northwestern Dent F_2 recombination yielded 16.6 per cent more than commercial Northwestern Dent and appeared superior to Northwestern Dent in the field.

It is recognized that, before recombining selfed lines for the purpose of producing improved varieties, it is necessary to determine the yielding ability of all F_1 combinations. Selfed lines which combine favorably with all others that are to be used should then be used for the recombinations.

What are the Possibilities of the Newer Methods?—Further extensive studies are necessary and are being conducted cooperatively by the Corn Belt stations and in other sections. A comprehensive plan of corn improvement has been drawn up with the view of further intensive

study of the physiology and genetics of the corn plant. By the application of such knowledge it should be possible to produce results which by the older methods could not be obtained. Harmful diseases such as root, ear, and stalk rots and smut can be controlled by producing resistant varieties. Considerable data are available to prove that selfed lines

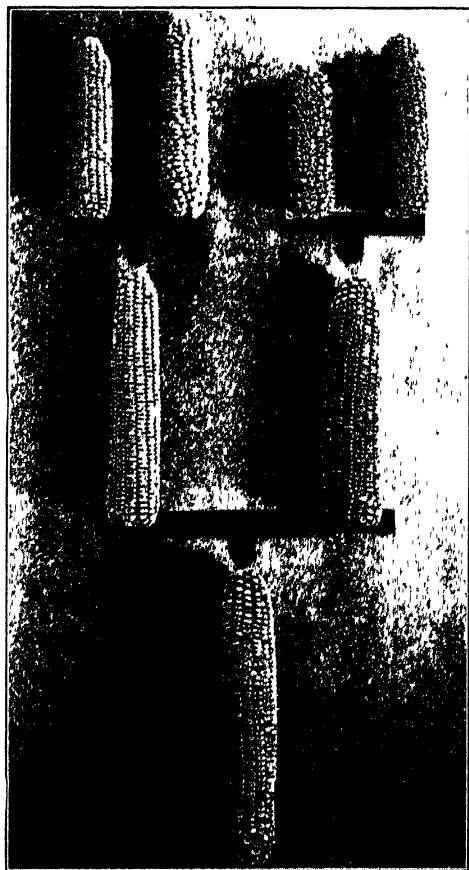


FIG. 53.—Average yields of 4 self-fertilized corn strains above, F_1 crosses in the center; the double cross below (After Jones)

and hybrids differ markedly in their reaction to particular conditions (Dickson and Holbert, 1926; Hoffer, 1926; Kiesselbach, 1926). The production of varieties or F_1 hybrids which excel in particular characters and which are adapted to particular soil and climatic conditions will result from a knowledge of the manner of reaction of selfed lines to particular conditions.

CHAPTER XVII

GRASSES, CLOVER, AND ALFALFA

The importance of hay crops in the world's agriculture makes desirable their consideration from the standpoint of improvement by breeding. Grasses, clover, and alfalfa differ strikingly in amount of seed set when artificially self-pollinated (see Chap. V). Red clover (*Trifolium pratense*) is rather highly self-sterile; white clover (*Trifolium repens*) sets few seeds when protected from insect pollination; timothy (*Phleum pratense*) contains both self-sterile and self-fertile lines; and brome grass (*Bromus inermis*) under a bag sets seed abundantly. Although common alfalfa (*Medicago sativa*) and yellow alfalfa (*M. falcata*) cross freely, seed of either may be produced by selfing. Enough examples have been cited to show that there are not only differences in the modes of pollination in the three mentioned classes of hay crops but also differences within each class. Carefully controlled experiments with grasses to determine the percentage of naturally crossed and naturally self-fertilized seed are very limited. When self-sterility is not a limiting factor, the methods of breeding all these crops are essentially alike. The ease with which some of them may be clonally reproduced has led to slight modifications in breeding technic. In the following brief discussion, the aim has been to choose a few examples rather than to enter into an exhaustive treatment of the entire field.

GRASSES

Timothy ranks far ahead of the other grasses in importance. Some of the other hay grasses which may be mentioned are orchard grass (*Dactylis glomerata*), tall oat-grass (*Arrhenatherum elatius*), and brome grass (*Bromus inermis*). These three grasses are adapted to certain conditions better than timothy is. Some important pasture grasses are Kentucky bluegrass (*Poa pratensis*), Canada bluegrass (*Poa compressa*), and redtop (*Agrostis alba*).

The variability (see Fig. 54) of each of the different species of grasses presents a wealth of material for breeding purposes. Moreover, the fact that many of them may be conveniently propagated as clones facilitates a study of the value of individual plant selections. The hereditary constancy of forms so isolated may be tested by selfing or by adopting methods which insure close breeding.

Breeding Timothy.—The United States Department of Agriculture has carried on extensive experiments in timothy breeding at New London and North Ridgeville, Ohio. As a result of breeding, two improved varieties have been widely distributed through the Ohio Experiment Station. The Cornell and Svalöf Experiment Stations have done considerable timothy breeding

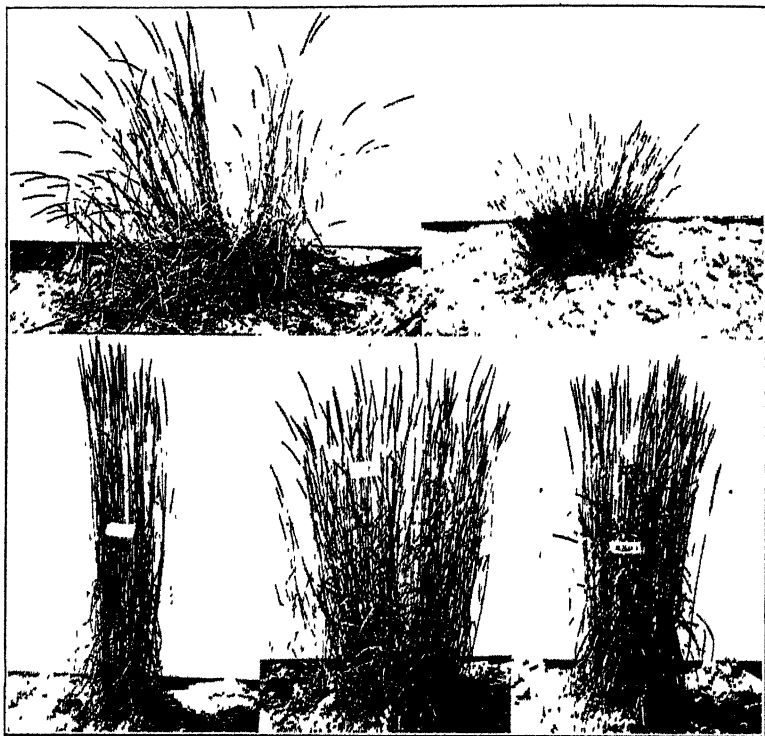


FIG. 54.—Individual timothy plants grown under like conditions. The upper plants are undesirable, one having weak stems and the other lacking vigor. The lower plants are more desirable. They differ in density of plant and number of culms. (Courtesy of Myers.)

Webber *et al.* (1912) published a detailed report of the experiments as carried on at Cornell. Samples of timothy seed were procured from various sources in the United States, Canada, and other countries. This seed produced an abundance of different forms from which selections

FIG. 55.—Flowers of timothy.

1. Spike.
 2. Floret—*a*, anther; *b*, filament; *c*, branched stigma; *d*, style; *e*, ovary; *f*, outer glume.
 3. Outer glume.
 4. *a*, feathery stigma; *b*, style; *c*, ovary.
 5. Spikelet showing *a*, palea; *b*, floral glume. (After Beal after Trinius and Scribner.)
- Size: 1, $\frac{1}{2}$ n; 2, 80n; 3, 4, 5, greatly enlarged.

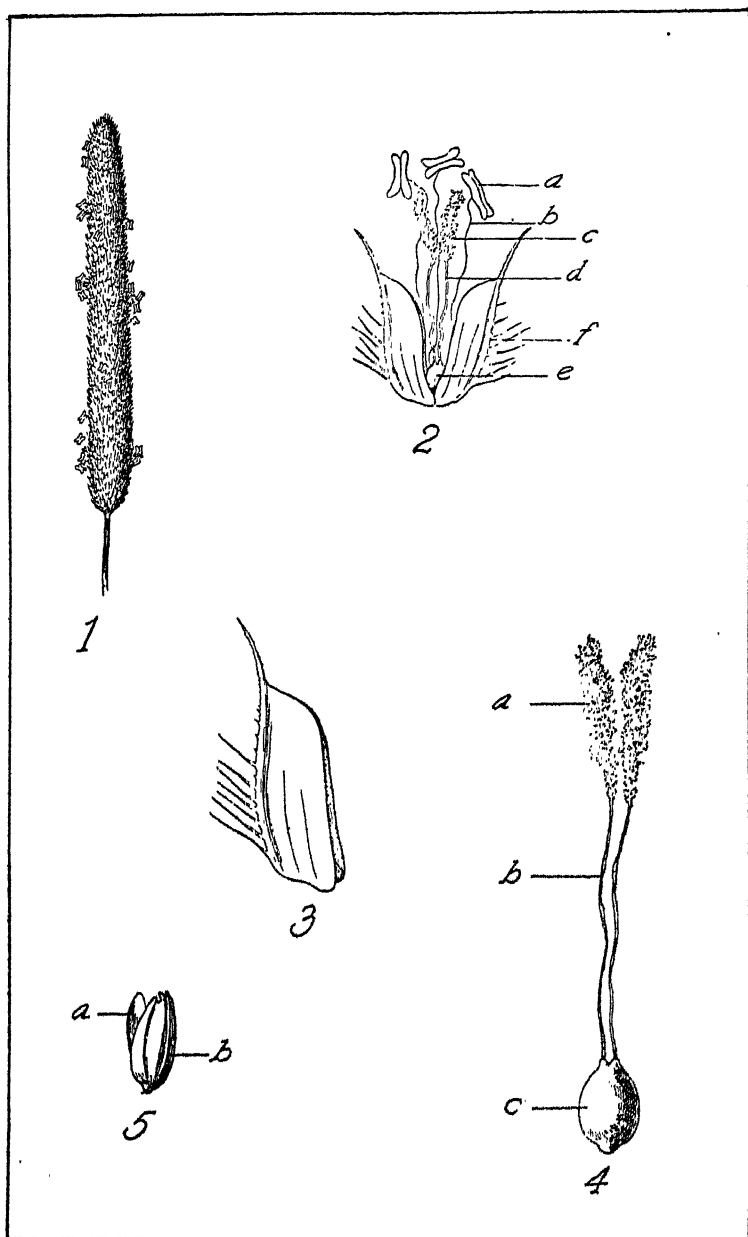


FIG. 55.

were made. Individual plants were selected on the basis of the following characters:

1. High-yielding ability
2. Height
3. Broad and thick plants, which stool abundantly.
4. Many and dense culms
5. Erect, non-lodging plants.
6. Many large leaves
7. Leaves extending well toward the top of the plant
8. Leaves remaining green until plant is nearly ready to harvest.
9. Rust resistance
10. Spikes of medium size, setting seed freely.

The ultimate aim was to produce a high-yielding variety. A selected plant was dug up and vegetatively propagated by separating bulblets from it. The bulblets were set out in rows (16 to 24 per row) and allowed plenty of space for individual development. Self-fertilized seed from these various clones was planted in sterilized soil and the seedlings were transplanted in rows as above. By a comparison of these rows and the respective clones from which they came it was found whether they were breeding true for the characters desired. When sufficient seed was available, plots were sown broadcast and yields obtained. As soon as a form appeared valuable and bred comparatively true, it was isolated and increased.

According to Webber, self-fertilized seed may be produced by placing several spikes of the same plant, just before blooming, under a paper bag. Another method is sometimes used in clonally propagated rows. Each row is surrounded by a fence about 10 feet high made of finely woven cloth. This method does not prevent some cross-pollination but it does bring about a high degree of inbreeding. A tall growing crop, such as rye, surrounding isolated plots prevents pollination with undesirable strains or varieties.

Witte (1922) obtained seed from timothy spikes isolated under parchment bags. At the Minnesota Experiment Station considerable variation in amount of seed set among self-pollinated plants was found. That this variation had a genetic basis was shown by the high correlation ($r = +0.820 \pm 0.033$) obtained between the amount of selfed seed set on individual plants in 1923 and the amount of selfed seed set on several plants of the respective progenies grown in 1924.

It has been pointed out by Hayes and Clark (1925) and by McRostie (1924) that self-fertilization in timothy does not lead to as great a reduction in vigor as has been observed in maize. Some selfed lines yielded less and others considerably more than the average of the commercial variety. Abnormalities have been reported among the progeny of self-fertilized individuals and, therefore, it seems that self-fertilization in

timothy as in corn is a logical means of eliminating undesirable characters and obtaining strains which excel in such important characters as yielding ability and disease resistance.

As would be expected in dealing with a heterozygous crop, the self-fertilized seed of isolated clones produce plants which show considerable difference in their inheritance. Some clones breed fairly true when reproduced by selfed seed, others do not. The following table, taken from Webber *et al.* (1912), illustrates the transmission of yielding ability in some clones.

TABLE LXXVII.—TRANSMISSION OF YIELD IN TIMOTHY BY CLONAL AND SEED PROPAGATION

Number of original plant	Plot No.	Average yield per plant of mother by clonal propagation, ounces	Plot No.	Average yield per plant of progeny by self-fertilized seed propagation, ounces
Light-yielding Plants				
12.07	1,797	1.005	3,216	2.121
9.03	1,713	1.830	3,109	3.364
104.30	1,794	1.982	3,213	4.071
191.19	1,785	2.283	3,142	3.143
811.02	1,728	2.542	3,166	1.925
128.19	1,799	2.462	3,217	0.966
211.31	1,792	2.806	3,211	1.905
212.36	1,653	2.811	3,143	4.140
8.04	3,011	2.941	1,959	3.714
107.30	3,033	3.158	1,960	1.182
Heavy-yielding Plants				
271.26	1,660	13.521	3,152	11.455
887.10	1,620	13.783	1,905	7.600
875.30	1,752	13.811	3,182	7.915
224.15	1,619	14.133	1,904	9.000
860.30	1,744	14.517	1,934	7.636
820.27	1,740	15.587	3,206	10.844
860.25	1,743	15.970	1,931	9.428
889.31	3,189	16.000	3,190	9.043
245.28	1,796	16.308	3,215	9.457
37.31	1,630	20.274	3,122	7.636

The practical results which have been attained by this method of breeding are brought out in the following table, also taken from Webber *et al.*

TABLE LXXVIII.—SUMMARY, SHOWING YIELD OF FIELD-DRY HAY

	Yield in pounds per acre	
	1910	1911
Average yield of 17 new varieties	7,451	7,153
Average yield of 7 checks	6,600	4,091
Actual average increase	851	3,062

The season of 1911 was particularly unfavorable for the growth of timothy. The new varieties gave a greater increase that year than in the preceding and more favorable one. Webber *et al.* attribute this difference partly to the rust resistance of the new strains.

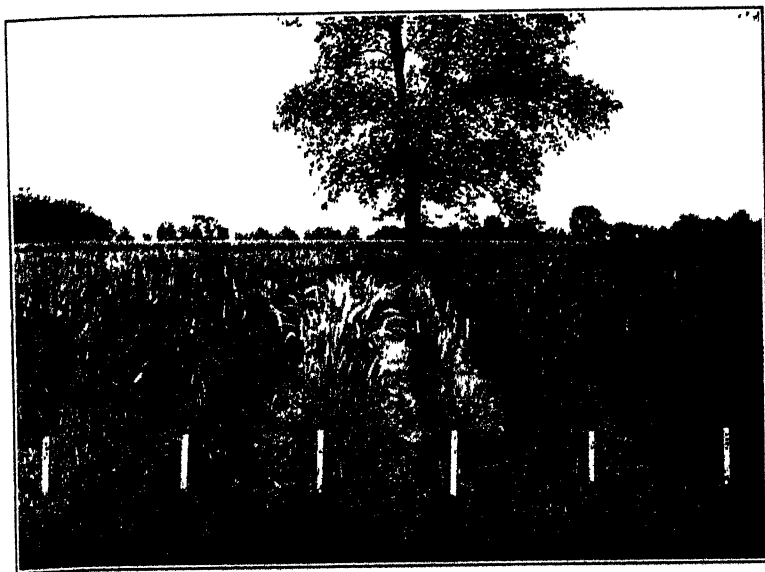


FIG. 56.—View of vegetatively propagated row plots of timothy. Each plot is propagated from a single, original plant. Note that the two central plots are comparatively late in maturity; also note differences between these two strains, one having erect culms and heads, the other having somewhat spreading culms and long, loose heads (Courtesy of Piper.)

The method of breeding timothy at Svalöf as reported by Witte (1919) is not essentially different from that practiced at Cornell. Individual-plant selections are vegetatively propagated in plots isolated as much as possible. Seeds produced by the better clones are planted in varietal plots for comparison. The best commercial varieties are also grown for comparison. When a new variety proves superior and has practical

uniformity, it is increased and distributed on a large scale. A comparison of ordinary timothy and two improved forms distributed by the Svalöf Station is shown in the following table (Witte, 1919):

TABLE LXXIX.—YIELD OF DIFFERENT VARIETIES OF TIMOTHY IN TRIALS AT SVALÖF, 1909-1918

Variety	Kilograms of green fodder per hectare			
	First year's lay	Second year's lay	Total	Yield per cent compared to ordinary Swedish timothy
Svalöf's Gloria.....	11.48	11.03	25.51	120.6
Svalöf's Primus.....	13.46	10.21	23.67	111.9
Ordinary Swedish.....	11.57	9.59	21.16	100.0

Timothy, like many other grasses, is susceptible to a rust (*Puccinia graminis*). It has already been mentioned that in making selections at the Cornell Station some attention was given to resistance to this fungus. Eleven of the better Cornell selections have been tested for rust resistance (Hayes and Stakman, 1919). The relation of other characters to resistance was also studied. The rust classes are: 1, no rust; 2, slight infection; 3, moderate infection; and 4, heavily rusted. Average erectness is taken with 1 as a basis of an erect plant and 10 a procumbent one. Table LXXX presents the data.

From the table it is apparent that the Cornell selections possess a high degree of resistance. Relatively few plants are found in rust classes 3 and 4. The Minnesota selections show the reverse condition, *i.e.*, most of the plants are found in classes 3 and 4. These facts show that a variety of rust-resistant timothy may be isolated.

In a later investigation, Barker and Hayes (1924) obtained evidence that resistance to rust in timothy was transmitted as a dominant character dependent on a single-factor difference for its expression. No evidence of the existence of more than one biologic form of *P. graminis phleipratensis* was found.

Timothy breeding may be briefly summarized as follows:

1. Individual plants propagated vegetatively in rows. Bulblets are placed far enough apart in the row to give ample room for individual development.

2. The clones produced in 1 are closely inbred or seed is saved from vegetatively multiplied plants in isolated plots. By planting the seed so produced clones are tested for transmission of the desired characters and also for uniformity.

3. When sufficient seed is available, plots are sown broadcast and tests for yield are obtained under ordinary field conditions.

4. A selection which has shown performance ability is increased in isolated plots and distributed to the farmers

It appears very probable that controlled self-pollination with selection in selfed lines is a valuable method to use in breeding timothy.

TABLE LXXX —RUST RESISTANCE IN TIMOTHY IN RELATION TO OTHER CHARACTERS AS SHOWN BY VARIOUS DATA

Variety	Rust classes				Rust mean	Average yield per plant, pounds	Erectness mean	Average length of head, centimeters	Average height, centimeters	Average number of stools
	1	2	3	4						
Cornell 1,611	80	11	1	0	1.1	1.0	2.3	11.9	88	122
Cornell 1,620	77	26	3	2	1.3	1.0	2.2	18.3	88	138
Cornell 1,630	79	15	9	2	1.3	0.9	3.1	12.3	85	111
Cornell 1,635	61	14	9	3	1.5	0.8	2.9	11.4	85	109
Cornell 1,671	56	13	13	5	1.6	0.8	2.9	11.6	89	123
Cornell 1,676	87	10	3	6	1.3	0.9	2.9	13.1	87	116
Cornell 1,687	86	12	9	6	1.4	0.9	3.7	11.3	88	131
Cornell 1,715	90	11	6	3	1.3	0.8	3.0	10.3	86	98
Cornell 1,743	100	3	12	7	1.4	1.0	5.6	10.9	84	134
Cornell 1,777	36	0	4	0	1.2	0.9	5.7	11.5	83	142
Cornell 3,230	32	5	5	0	1.4	0.9	3.1	12.9	86	117
U. S. Dept. Sel. 1.	2	12	70	40	3.2	0.6	2.6	13.0	91	64
U S Dept. Sel. 2	4	4	19	13	3.0	0.8	3.3	10.9	87	90
U S. Dept. Sel. 3	0	7	15	9	3.1	0.8	2.8	13.3	92	72
L L. May Sel. 1..	2	3	24	15	3.2	0.6	2.3	12.4	86	70
L L. May Sel. 2	8	5	25	6	2.7	0.6	3.1	10.1	80	92
Griggs Bros. Sel. 1..	1	1	15	5	3.1	0.7	3.0	12.8	86	91

Brome Grass.—Brome grass is a valuable hay and pasture plant, particularly in regions where the rainfall is limited and where cool weather prevails during the growing season. Waldron (1921*a, b*) has pointed out that clonal lines of *Bromus inermis* differ strikingly with regard to yield and percentage of protein. One of the high-yielding strains produced three times as much protein per acre as one of the low-yielding strains. Some positive correlation was obtained between percentage of protein and yield.

As brome grass produces seed abundantly under controlled, self-pollination conditions, it appears that selection in self-fertilized lines is a desirable method of breeding.

CLOVERS

The importance of clovers as forage crops and their rôle in soil improvement make them of great economic value. *Trifolium pratense*,

or ordinary red clover, is by far the most widely grown. Alsike clover (*T. hybridum*), because it may be grown in more acid soil than the other clovers, is favored in certain localities. Some of the other clovers are white (*T. repens*), crimson (*T. incarnatum*), Japanese (*Lespedeza striata*), and the sweet clovers (*Melilotus alba* and *M. officinalis*). All of these species are biennial or perennial except *T. incarnatum* and *L. striata* which are annuals.

Red Clover.—Early studies of pollination in red clover led to the belief that this species was practically self-sterile. More recent studies, particularly those of Fergus (1922), Williams (1925), and Kirk (1925), have shown that seed may be produced by self-pollination. These investigators have succeeded in isolating strains of red clover that are relatively self-fertile. Fergus self-pollinated 650 heads representing as many different plants and obtained 153 seeds from 32 heads. These were tested in the next generation and it was found that in general the seed from the more fertile heads produced progeny which again set considerable selfed seed. In a similar experiment Kirk obtained 430 seed from 230 heads of a Minnesota strain of red clover and 904 seed from 200 heads of a strain known as Altaswede. These experiments have shown that self-fertility in this crop has a genetic basis the same as has been demonstrated for other crops.

Westgate *et al.* (1915) found that moist soil and atmospheric conditions induced the formation of a large percentage of infertile ovules. All the cells remained sporophytic, no reduction taking place with the formation of an embryo sac. As much as 100 per cent ovule infertility was found in the first clover crop. The rate of pollen-tube growth was shown to be much slower in the self- than in cross-pollinated plants. It is probable that in many cases pollen-tube growth is too slow to effect fertilization when the plant is selfed. The pollen of red clover is easily burst by an excess supply of moisture. Martin (1913) demonstrated that good artificial germination of pollen could be obtained on membranes which were just moist enough to regulate properly the supply of water to the pollen. He suggests that the stigma of red clover performs the same function as the membranes.

Inheritance.¹—The studies of Kajanus and of Gmelin show that the leaf markings (light-green portion) characteristic of red clover are inherited and that there are at least two factor differences involved. Likewise, the tendency to produce supernumerary leaflets has been shown to be an inherited character although its expression is very much influenced by soil productivity—polyphyly is greater on plants well

¹ A review by MALTE (1921) has been freely used in the following discussion. Where no literature citation is made the reference is to this article. MALTE, M. O., "Variation and Inheritance in Red Clover," *Sci. Agr.*, vol. 2, pp. 79-83, 125-132, 157-162.

nourished. After practicing selection for several years, DeVries isolated a form which had a tendency to produce supernumerary leaflets and which he called *T. pratense quinquefolium*.

The inheritance of flower and seed color has been investigated by several plant breeders. Red flowers were found dominant to blue by Kajanus. Malte concluded that red flower color was probably dependent on two or more factors. As a result of studies of seed color, Kajanus found that dark purplish was dominant over light purplish and that both were dominant over yellow. These results indicate that varieties of clover breeding true for seed color may be produced.

The occurrence of seedlings deficient in chlorophyll in the progeny of self-fertilized plants has been noted by Fergus (1921) and by Kirk (1925). The former reported deficient seedlings in 1 out of a total of 32, whereas the latter found deficient seedlings in 21 out of a total of 81 self-fertilized lines.

Disease-resistant Clover. Clover anthracnose (*Colletotrichum trifolii*) causes serious injury to red clover in certain regions. Bain and Essary (1906) issued a preliminary report on isolating an anthracnose resistant red clover. Healthy plants in a badly infested field were located late in the season after most plants had been killed by the disease. The seeds of the chosen plants were planted separately in alternate rows with ordinary commercial seed. Measures were taken to insure the infection of every seedling with anthracnose. By June 1 the commercial plants began to show symptoms of the disease and by the middle of September not more than 5 per cent of them were living, while 95 per cent of the selections were healthy and making a fair average growth. Some of the latter showed small lesions, but growth was not seriously affected. By continuing these investigations, a strain of red clover has been produced which is resistant to anthracnose. The Tennessee Agricultural Experiment Station has distributed seed of this strain to farmers. It is proving to be of much value.

A fungus disease which frequently attacks red clover is powdery mildew. Mains (1922) has pointed out that this fungus is not commonly found on *T. incarnatum*, *T. hybridum*, or *T. repens* and that there seems to be considerable difference in the degree of resistance to this disease among individual plants of *T. pratense*. In general, the American varieties of red clover proved more susceptible to mildew than European varieties.

The reaction of several species of *Trifolium* to *Brackysporium trifolii* under certain conditions in a greenhouse has been studied by Bonar (1924). *T. incarnatum* was found highly susceptible and *T. pratense* and *T. repens* moderately susceptible to this disease.

Adaptation.—Investigations have been carried on by a number of experiment stations to determine the relative adaptability of red-clover

strains from different regions. In general, seed produced locally has given more satisfactory results than imported seed. Christie (1923) found that Indiana and Ohio strains of red clover withstood Indiana winters whereas three strains from Italy, four from Chili, one from Bohemia, one from Hungary, four from France, and two from Germany all winter killed more or less. In a somewhat similar experiment conducted in Michigan, Cox and Megee (1924) found that seed grown in Michigan and in the northern states or Canada was more dependable and better adapted than seed from other sources. Seed from western Oregon and Italy was of practically no value whereas seed from northern Europe and Chili in some cases gave good results. Similar results were obtained by Army (1924) in Minnesota. Farther south in the general region of Tennessee, Kentucky, Virginia, West Virginia, and Maryland, anthracnose is frequently the cause of failure with red clover; therefore resistance to this disease in addition to general climatic adaptation is highly desirable.

Breeding.—The improvement of red clover may be accomplished by one of two methods of breeding, namely, a restricted form of mass selection or self-fertilization followed by hybridization and selection. In either case it is desirable to first make a comparison of the varieties produced by other breeders and of commercial seed from different sources to obtain the best forms for the foundation stock. In mass selection, a seed plot may be used in which each plant is spaced so that its characters may be determined. Undesirable plants should be removed before pollination. By repeating this process, forms with the desired characteristics and with practical uniformity may be isolated.

The studies concerning self-fertilization in red clover which have been mentioned show that it is possible to produce relatively homozygous lines by artificial self-pollination. The pure strains which show the desired characters may then be crossed and selection made among the progeny in a manner somewhat analogous to the modern method of corn breeding.

Japanese Clover.—According to Essary (1921), Japanese Clover, *Lespedeza striata*, was first described in Georgia about 1816 where it is thought to have been introduced accidentally as packing for goods shipped into the United States. It is a native of eastern Asia.

In 1912, the Tennessee Experiment Station made 258 selections from both wild and cultivated *Lespedeza* plants. Some were individual-plant selections and others were selections made from groups of plants. It is stated that the progeny of individual plants "have remained true to type to a remarkable degree." As a result of this work three new strains of *Lespedeza* have been developed. One of these strains is adapted for hay, one for pasture, and one for growing in sections of Tennessee where the season is relatively short.

Sweet Clover.—The sweet clovers have been known for many years although it is only recently that their agricultural value has been recognized. In addition to the yellow- and white-flowered biennial sweet clovers, an annual white-flowered form exists, to which attention was called by Prof. H. D. Hughes of the Iowa Agricultural College. In the biennial sweet clover (Pammel and King, 1918) the upper portion of the underground organ is a stem and produces numerous buds. These are absent in annual sweet clover.

Aberrant forms in Arctic sweet clover have been reported by Kirk (1924). The aberrant plants were found in a variety that 3 years previous had been grown in a long, narrow field adjacent to a similarly shaped field of Grimm alfalfa. A further study of these unusual individuals (Kirk, 1926) showed that some of them were completely sterile, others nearly so, and some were completely fertile. Thirty-four seedlings from each of ten fertile plants were transplanted to a field. Six of the families showed segregation into two distinct types: one similar to sweet clover and another with greater leafiness, numerous stalks, and a well-developed, much-branched crown, somewhat similar to alfalfa. The coumarin content among the plants of the latter type varied and in some plants it was almost completely absent. It is suggested that these aberrant forms may have arisen as the result of a natural cross between sweet clover and alfalfa.

ALFALFA

Alfalfa is one of the oldest, if not the oldest, plant cultivated for its forage only (Piper, 1916). Most of the cultivated forms belong to the species *Medicago sativa*. The only closely related species of economic value is *M. falcata*, sometimes called sickle alfalfa or yellow-flowered alfalfa. The two species cross readily, as Waldron (1919) has shown (for pollination studies on alfalfa, see Chap. V). Piper *et al.* (1914) found that alfalfa set more seed when cross-pollinated than when selfed, although the selfed set considerable seed. It also was demonstrated that automatic tripping with consequent self-pollination may occur under certain conditions.

Grimm Alfalfa and Winter Hardiness.—Westgate (1910) and, later, Brand (1911) suggested that the origin of Grimm alfalfa was probably the result of natural crossing between cultivated alfalfa (*M. sativa*) and

FIG. 57.—Structure of alfalfa flowers.

1. Branch showing flowers in position.
 2. Single flower, showing—*a*, standard; *b*, sexual column in contact with standard; *c*, keel; *d*, wings.
 3. Seed pod.
 4. Flower parts in position—*a*, undeveloped pod; *b*, ovary; *c*, filament; *d*, anther.
 5. Same with all anthers removed except one to show stigma.
 6. Anther.
- Size: 1, about $\frac{1}{2}n$; 2, about $2n$; 3, about $\frac{1}{2}n$; 4, 5, 6, greatly enlarged.

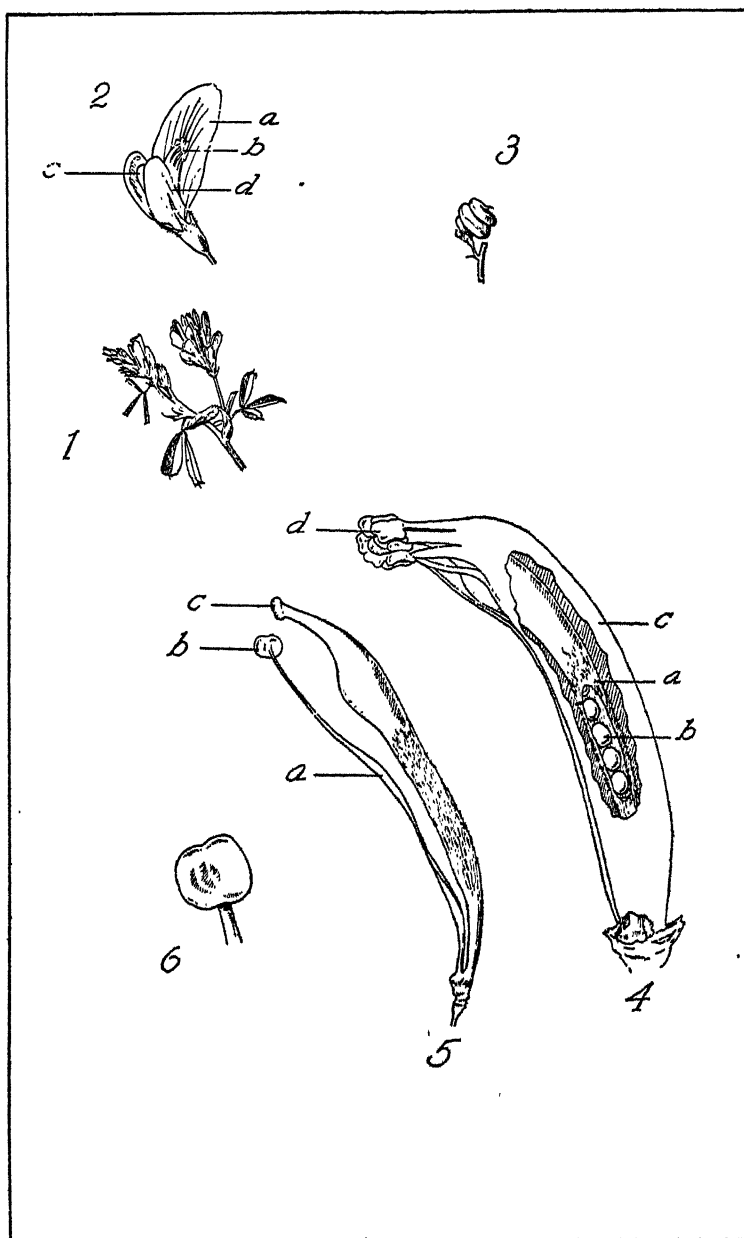


FIG. 57.

wild plants of the yellow-flowered sickle lucern (*M. fulcata*) found especially in Germany, Austria, Roumania, and certain regions of Italy. The seed from which the Grimm variety eventually resulted was brought to Carver County, Minnesota, by a German immigrant farmer, Wendelin Grimm, in 1857. Here for 50 years the original variety was subjected to the severe Minnesota winters and as a result the non-hardy types were eliminated.

Waldron (1912) reported the result of testing for winter hardiness 68 different strains of alfalfa assembled from various parts of the world. The trial was made at Dickinson, N. D., during the severe winter of 1908 and 1909. The two strains of Grimm alfalfa included in the experi-

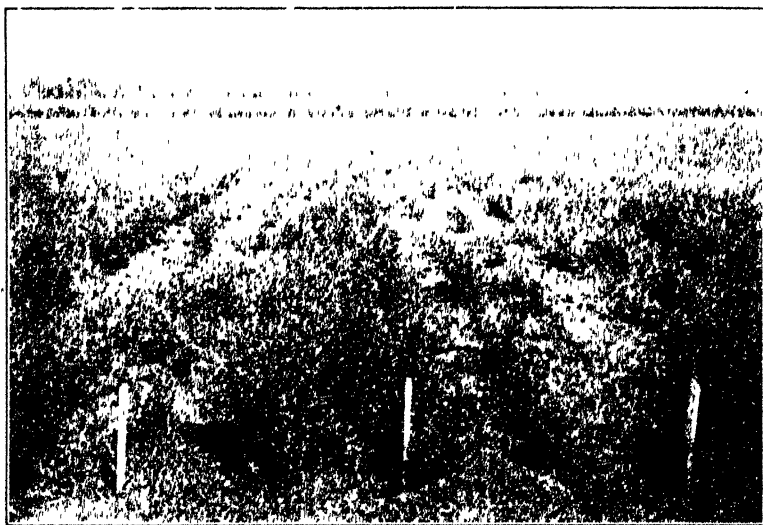


FIG. 58.—Comparative hardiness of Grimm and common alfalfas. The two rows in the center are from Grimm seed. At either side are rows grown from southern grown common seed. 1916 season. (Photo loaned by Army.)

ment proved to be the hardiest. On an average, less than 5 per cent of the Grimm plants were killed and only one other strain showed less than 10 per cent killed. Disregarding 12 strains which were destroyed completely, the average percentage killed for the other strains, considered as a unit, was 77.5.

To bring out the fact that differences between strains in their respective reactions to cold are genetic, Waldron computed correlation coefficients. Two nurseries had been planted on succeeding years with the same strains taken from the same original lot of seed. The percentage of killing of the various strains in one nursery during the winter of 1908 and 1909 was correlated with similar data collected from the other

nursery after the winter of 1910 and 1911. A correlation coefficient of $+0.62 \pm 0.06$ was obtained.

Some of the surviving plants of the different alfalfa strains were selfed and the seeds so obtained were planted separately in a third nursery. Percentage of winter killing of these strains was taken and the correlation coefficient between the percentage of winter killing of the parental stock and that of the new strains was determined. The correlation coefficient obtained was $+0.46 \pm 0.07$. The mean winter killing (expressed in percentage) of the parental stock was 27.43 ± 1.75 as compared with 6.43 ± 0.66 for the strains coming from selfed seed. In other words, progress has been made toward isolating hardy biotypes.

Other winter-hardy strains of alfalfa have been developed by the Michigan (Spragg and Down, 1922) and the Saskatchewan (Kirk, 1924) agricultural experiment stations. Two strains developed at the latter station were produced by selection from Grimm. One of these strains is superior in yield of hay and the other excels in yield of seed. The new strain produced at the Michigan Station has been named Hardigan. In addition to winter hardiness it possesses a satisfactory yielding capacity of both hay and seed when grown in Michigan. It is resistant to leaf spot also.

CHAPTER XVIII

POTATO IMPROVEMENT

Potatoes have been brought into general cultivation since the discovery of America, and are now a crop of major importance in many countries. As potatoes are reproduced commercially by tubers, they furnish an excellent illustration of the way in which vegetative reproduction modifies breeding methods.

Origin and Species.—There are from 5 to 100 species of tuber-bearing potatoes according to the number of forms which are recognized as separate species (East, 1908*b*; Wight, 1916). Whether the cultivated potato arose from a single wild species or from several is a debatable question. The preponderance of opinion is that there is only a single wild species, *Solanum tuberosum* L., which deserves to be considered as the stem form from which all cultivated varieties arose. Wight (1916), after carefully examining herbarium material, previous records, and wild species, makes the following statements:

Every reported occurrence of wild *S. Tuberosum* that I have been able to trace to a specimen, either living or preserved in the herbarium, has proved to be a different species. I have not found in any of the principal European collections a single specimen of *Solanum tuberosum* collected in an undoubted wild state.

Berthault (1911) cites Heckel, Planchon, and Labr gerie as examples of recent workers who believe that other wild species gave cultivated *S. tuberosum* forms by mutation; Planchon, believing that the original form was *S. commersonii*; Heckel, that *S. maglia* through mutation produced cultivated potatoes; while Labr gerie believed both of these species gave cultivated forms through mutation. Berthault attempted to answer the question by growing seeds and tubers of both these species and also by growing seed of several cultivated varieties. Progeny of seed or tubers of *S. maglia* and *S. commersonii* gave no forms which approached in calyx or corolla characters the cultivated varieties of *S. tuberosum*. Progeny of seed of cultivated varieties showed Mendelian segregation, but no characters were obtained which had not been observed in ancient cultivated varieties. Wittmack (1909), after a careful botanical study of species, reached the conclusion that *S. tuberosum* was the stem species from which all cultivated potatoes arose.

This conclusion is further justified by a summary of results of species crosses given by Fruwirth (1925). Not all of the crosses were successful, but, in general, crosses between different forms of *S. tuberosum* were less

difficult to obtain than those between *S. tuberosum* and the other tuber-bearing species.

The evidence presented by De Candolle (1886) seems sufficient to prove that the potato grew wild in Chile in a form which is very similar to that of our cultivated plants. Heckel (1912) reports a study of changes under cultivation of forms of *Solanum tuberosum* collected in the wild in Bolivia and Peru by M. Verne. The wild plants were 0.25 meters in height, with blue flowers, deep green foliage, and tubers about the size of a hazel nut each produced at the end of a long root-stalk. These tubers were planted at Marseilles in a garden heavily fertilized with manure. There was little change in the flower and fruit characters but there were pronounced changes in the subterranean parts. The yellowish tubers, each borne at the end of a much shortened root-stalk, contained a far greater amount of starch than wild tubers, and the characteristic bitter taste of the wild tubers disappeared. Much more profound changes in tubers of *S. maglia* occurred under cultivation (Heckel, 1909).

There seems to be no good reason for speaking of all these tuber changes as mutations. It is more in line with modern genetic usage to consider them as the normal expression of the inherited factors under the new conditions of environment which occur under cultivation.

The cultivated potato was first introduced into Spain and Portugal by the Spaniards during the first half of the sixteenth century.¹ A description and illustration of the potato, published by Clusius in his "*Rariorum Plantarum Historia*" in 1601, were made from a plant sent him, in 1588, by the governor of Mons. The flowers were light purple and the original plant obtained by Clusius produced a fruit ball and two reddish tubers. From this introduction the potato was taken probably into Italy, from there early in the seventeenth century to Austria, then to Germany, from Germany to Switzerland, and finally to France.

Drake, after a West India piratical trip, took the Roanoke colony, including Thomas Herriott, to England. Probably potatoes were part of the stores obtained in the West Indies by Drake and these Herriott introduced into Ireland about 1586. This was the second introduction into Europe. It is generally believed that the English colonists of Virginia and Carolina first obtained the potato from Spaniards or from other travelers. Gerard described and illustrated a variety of potatoes in his "*Herbal*" in 1597. This variety had light-brown to yellowish tubers and violet to almost white flowers.

Inheritance of Important Economic Characters.²—Systematic plant breeding with the idea of combining the desirable characteristics of two

¹ East, 1908b.

² This discussion and the more detailed one at the end of the chapter is based on inheritance studies made by several investigators, particularly SALAMAN and EAST and summarized by FRUWIRTH (1925). Where author without date of publication is cited, reference is made to Fruwirth's summary.

parental varieties can be carried out only after the breeder has familiarized himself with the characters of particular varieties and of their wild relatives. Varieties which are otherwise desirable, however, frequently are lacking in some particular character. Thus a variety with the period of maturity of Early Ohio but with less tendency to second growth would be of material value, while a variety similar to Irish Cobbler but with shallower eyes appears desirable. A late-maturing variety for the South with as great heat resistance qualities as McCormick and with good tuber type, such as Rural New Yorker or Green Mountain, would be a valuable addition to the potato varieties for that section. The discovery of the wart disease in the United States and the knowledge that certain American varieties are susceptible, has given some impetus in this country to the breeding of wart-resistant varieties. Thus, with the potato, as with other crops, the breeder should first determine the ideal toward which he will work. Parental varieties should then be selected because of some desirable characters. By recombination of the favorable characters of both parents, improvements may be obtained. The transmission of potato characters through the seed is in conformity with Mendelian principles. Vegetative propagation allows the breeder to perpetuate any desirable genotype even though heterozygous, which is the usual condition in the potato plant. While, in general, self-fertilization of a commercial variety gives rise to seedlings which vary a great deal, it is comparatively easy to obtain homozygosity for some characters.

Tuber shape and depth of eyes are important characters which are used as one means of varietal classification. Tuber shape has been found to depend essentially on the presence or absence of a single factor for length. According to this hypothesis a tuber may be homozygous long, homozygous round, or heterozygous long. Heterozygous long is the most variable of the three conditions. In one experiment two varieties with round tubers when selfed produced nothing but round tubers, while twelve varieties with oval tubers, when selfed, produced long, oval, and round-tubered progeny. Heribert Nilsson (1912-1913) found one variety of potato that did not breed true for round tubers. Long tubers were dominant to round in Fruwirth's (1912) experiments.

Conflicting results with regard to the inheritance of depth of eyes have been obtained. Salaman (1912-1913) and East agree that shallow eyes are the dominant condition, whereas Heribert Nilsson thought that deep eyes were dominant over shallow eyes. Small round eyes were found to behave as recessives to large broad eyes.

Salaman (1925) reported a study of inheritance of "cropping index." This index was devised to express the ratio of haulms (vines) to tubers. Twenty-five thousand seedlings from four hundred families were studied and by estimation the plants were placed in five classes. Class 1 contained the plants with the greatest tuber weight in proportion to haulms

while class 5 were "zero croppers" or almost without tuber formation. Classes 2, 3, and 4 were of intermediate condition. Vigor of plant did not appear to be correlated with cropping index although, in general, the more vigorous the plant the greater the tuber formation. It was suggested that two cumulative factors *A* and *B* controlled cropping index, and that the highest genetic composition of a normal variety was *AaBB* rather than *AABB*. The latter genotype was considered sterile while the double recessive *aabb* represented the formula for a zero cropper. Certain wild types crossed with high-producing domestic varieties produced all zero croppers in F_1 . This result was considered to indicate the presence in the wild types of dominant inhibitors of *A* and *B*. The possibility should not be overlooked that cropping index may be correlated with earliness, a character which Krantz observed strongly influenced tuber production. Certain late-maturing seedlings produced a very small crop of tubers and this was believed to be because the season was not sufficiently long to permit complete maturity.

The inheritance of habit of growth in the potato has been reported by Salaman and Lesley (1920). Three distinct forms, namely, upright, procumbent, and prostrate, were described. The prostrate habit of growth, in which the vines sprawl along the surface of the ground, is recessive to the upright form and differs from it by at least two and probably three factors. The procumbent plants are intermediate between upright and prostrate. The genetic relationship of this character has not been established but the authors have some evidence that it is a recessive and differs from upright by a single factor. There was some indication that the prostrate forms could better endure drought than the upright types.

Sterility of the anthers has been found to be a dominant character. Salaman believed at first that its inheritance was due to a single differential factor pair but later evidence indicated a more complex manner of transmission. More recently Salaman and Lesley (1922) have reported a detailed study of pollen sterility. When the pollen grains were of good size and abundant, the plant was classed as a fertile pollen producer but when they were small, less abundant, or almost wanting, the plant was classed as sterile. Three varieties of potatoes, Edzell Blue, Myatt's Ashleaf, and Edgecote Purple, were used in the study. Edgecote Purple and Myatt's Ashleaf both, when crossed reciprocally or selfed, produced offspring which were classed as "fertile." Edzell Blue, when selfed, produced both fertile and sterile offspring but when it was used as a pollen parent in crosses with Edgecote Purple, all plants of the F_1 and F_2 generations were fertile. In reciprocal crosses, approximately half of the offspring were fertile and half sterile. It was suggested that somewhere in the lineage of the formation of pollen the basis of sterility had been lost whereas in the lineage of the formation of egg this had not occurred.

Pollen sterility, therefore, appears to be dominant to fertility although sterility is transmitted only through the eggs. This is a very important conclusion for the practical breeder. No variety would be homozygous for pollen sterility and lines homozygous for fertility could be produced by self-fertilization and selection if offspring could be obtained.

Besides this type of hereditary sterility which, according to Dorsey (1919), Breeze (1921), and Young (1922), occurs after the formation of tetrads and the pollen grains have assumed their characteristic form, degeneration takes place in the pollen mother cells prior to the period of tetrad formation, due, it is believed, to external environmental causes. This may result from insufficient nourishment or "infestation of amoebae or other microorganisms."

The transmission of immunity to wart disease has been studied by Salaman and Lesley (1923). Immunity behaves as a dominant although this dominance may be inhibited by other factors. Four types of immune plants were obtained. One type bred true, the other three, when selfed, gave ratios of 15:1, 3:1, or 9:7, respectively.

Inheritance.—Several factors, in addition to the chromogen body, have been recognized in tuber coloration. Red potatoes contain two genes, *R*, a reddening factor, and *D*, a developer of pigment. Purple and black tubers have, in addition to *R* and *D*, another factor, *P*. Segregating ratios were in accordance with the above factorial hypotheses. Wilson (1916) obtained only white tubers from selfed white-tubered varieties. Similar results have been obtained by other plant breeders which show that white is a recessive character. Recently Collins (1924), Kelley (1924), and Krantz (1926) have studied the inheritance of tuber color pattern. The explanation made by Krantz will account for the results obtained by Collins and Kelley and is therefore given here in some detail. Three factor pairs were involved in the development of color in the tuber. The factor hypothesis used was as follows:

D is a basic color factor necessary in the dominant condition for the development of color in the tuber skin.

R is a factor which, when present with *D*, leads to the production of parti-colored tubers.

A is a factor which, when present with *D* and *R*, produces suffused or self color.

The selfed progeny of Red McCormick, Triumph, and Early Ohio were studied, as well as crosses of a recessive white strain, U. S. D. A. seedling No. 14,329, with Triumph and Early Ohio. It was concluded that Triumph probably has the genetic composition *DDRRaa*, Early Ohio *DdRrAA*, Red McCormick *DdRrAa*, and the white seedling *ddrraa*.

Fruwirth (1912) found yellow flesh of tuber dominant over white. It was also found that different gradations of color were inherited. Heribert Nilsson (1912-1913) observed that some varieties with yellow flesh (tubers) bred true when selfed, others segregated as dihybrids with white recessive. Evidence that several factors were operating in the inheritance of tuber flesh color was obtained.

A certain amount of coloring in the young sprouts or shoots, stems, and sometimes in the leaf petioles was found associated with the presence of color in the tubers. With regard to flower color, three white-flowered varieties, selfed, produced only white flowers; and three out of four colored varieties, when selfed, produced both colored and white forms. Color is, therefore, dominant to its absence. Inheritance of this

character may be explained by assuming the presence of a chromogen body and modifying factors. Heliotrope flowers are due to the chromogen body plus a reddening factor; purple flowers are produced by the addition of a purpling factor; white flowers may be due to the absence of one or more of these factors.

It appears that, in many cases, quantitative characters are dependent upon multiple factors. McDougal (1917) crossed the wild potato of Arizona, *S. fendleri*, which grows at a high altitude and endures extremes of climate, with a domestic variety. The wild form produces small tubers. In the F_2 generation, forms appeared which were identical with the wild parent together with many intermediate types. Krantz (1924) found that F_1 varietal crosses were, as a rule, more vigorous than the seedlings obtained from the selfed seed of the parents. Second generation seedlings were less vigorous than first generation seedlings probably owing to the fact that the former were on the average more nearly homozygous. The facts support the theory that these quantitative characters are dependent upon multiple factors.

Production of New Forms.—For the purpose of differentiating between two important phases of potato improvement, Stuart (1915) has referred to "selection" as the "isolation and asexual propagation of desirable strains or types" while "breeding" is used only for sexual reproduction. With certain crops, such as the potato, this terminology is distinctive. Such a restricted usage of the word "selection" seems undesirable. The same idea can be obtained by the use of "clonal selection" to refer to the asexual propagation of desirable strains or types. Sexual breeding is the most promising method of obtaining new varieties although clonal selection has an important place in keeping the variety in a state of purity and in the control of certain diseases. Modern methods of sexual breeding and certain difficulties involved will be discussed briefly.

The Difficulties of Obtaining Crossed Seed.—The technic of making a cross is very simple. Several flowers in the same cluster may be pollinated about the same time. Unopened buds may be emasculated, pollinated immediately, and seed frequently is obtained. Stuart (1923) collected flowers to be used as the male parent in small sacks. The following description of the technic of pollination was given:

The corolla is pushed back between the thumb and forefinger of the left hand and held in such a position that the anthers extend upward toward the thumb nail. After removing the pistil the anthers are tapped sharply with the forceps, thus jarring the pollen out of the terminal pores, upon the thumb nail, on which it is readily conveyed to the stigma of the previously uncovered flowers.

The flowers are receptive two to four days after emasculation. East (1908a) concluded that the potato was usually self-fertilized. He also observed the fact that insects were seldom seen to visit the flower. Salaman (1910-1911) believes it unnecessary to cover the flower before or after pollination. Stuart, however, used 1-pound bags and found that if a certain amount of foliage was included in the bag its use did not cause a lowering of the number of seeds set. An average of between one and two hundred seeds was obtained by Stuart from each successful cross. The

difficulties of obtaining crosses are of three sorts. Some varieties are not free bloomers. Even though the variety is a free bloomer, environmental conditions may cause the flower to fall before seed is produced.

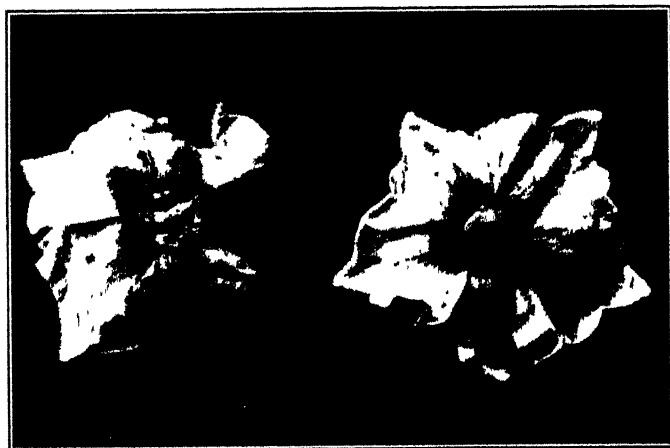


FIG. 59—Emasculated and unemasculated potato blossoms. (After Stuart.)

With some free blooming varieties, and under conditions favorable for blooming, the pollen production may be almost wanting.

Stuart (1923) states:

Most varieties will produce some blossoms when grown under optimum conditions for the normal development of the plant, particularly if these conditions prevail during the stage at which flower buds are formed. In many considerable varietal collections it is inevitable that many varieties should find the conditions unsuitable for their maximum development.

After studying numerous varieties Stuart made the following group classifications: Irish Cobbler, Early Michigan, Early Rose, Beauty of Hebron, Green Mountain, Rural, Peachblow, and Up-to-Date as profuse bloomers; Early Ohio and Burbank as moderate bloomers; and Triumph and Pearl as scant bloomers.

While all varieties produce flower buds the early dehiscence of these is the main reason why sparse bloomers are obtained. Perhaps in some cases, as pointed out by Breeze (1921) the early dropping of the flower buds may result from infestations of amoebae in the anthers. It was believed that some varieties were resistant to such infestations.

Stout and Clark (1924) have presented extensive studies of pollen sterility of many named varieties and of some wild species which were grown at Presque Isle, Maine. The varieties were placed in four classes although the description of the classes given here is much shorter than presented by them.

1. Pollen abundant, 30 per cent plump with 15 to 20 per cent of all grains which germinated.

2. Pollen abundant, 5 to 30 per cent of plump pollen, with only a few of these grains which germinated and usually with pollen tubes of feeble growth. Cross-pollination with varieties of this class produces little seed.

3. Pollen usually scant, but sometimes fairly abundant, percentage of plump grains 10 per cent or less, but rarely germinating. Cross-pollination with this class results in failure.

4. Pollen very scant, with scarcely a plump grain. No germination.

The pollen condition of some of the more important commercial varieties belonging to the various potato varietal groups summarized here has been adapted from their material. Classes 1 to 4 represent the four groups on the basis of pollen production and viability.

<i>S. tuberosum</i>	POLLEN CLASSES			
	1	2	3	4
1. Cobbler group.....	..	1	4	1
2. Triumph group.....	1	..
3. Early Michigan group.....	4
4. Rose group.....	3	2
5. Early Ohio group.....	2	..
6. Hebron group.....	3	..
7. Burbank group.....	3
8. Green Mountain group.....	..	5	6	..
9. Rural group.....	10	4
10. Pearl group.....
11. Peachblow group.....	1	1
12. Up-to-date group.....	6	1

Certain varieties were found to be dependable pollen parents. These were listed as follows: From the United States, Keeper and McCormick; from Canada, McIntyre; from Great Britain, Martin's Horn and Shamrock; from Germany, Olio; from Poland, Busola, Bohun, Switez, Zbyszek, Petronius.

Stuart (1923) calls attention to the inferior commercial characters of the four American varieties, Early Silver Skin, Keeper, McCormick, and Round Pinkeye, which were classed as dependable pollen parents while Clark (1923) and Krantz (1924) have urged the necessity of producing desirable pollen parents by selection in self-fertilized lines. Studies are already under way for the purpose of producing desirable homozygous pollen parent varieties. As was pointed out in the discussion of inheritance of economic characters, pollen sterility is a dominant character and transmitted only through the egg. By selection in self-fertilized lines pollen sterile individuals will become eliminated.

Methods of Handling.—Certain points regarding methods are of interest and have been taken from Stuart (1923). As soon as the seed balls are ripe, which condition can be recognized in most American varieties from the pale lemon-yellow color at this stage, the seed balls

should be removed from the vines. After harvesting the seed balls they should be crushed into pulp and placed in a vessel of water. In the course of several days fermentation will have set in and if the material has been stirred several times during this period the pulp will rise and can be removed easily. The seed should be collected and dried in which condition it may be held for several years.

When small amounts of seed are available the seed balls may be cut crosswise and the seed squeezed out on a piece of paper and left to dry.

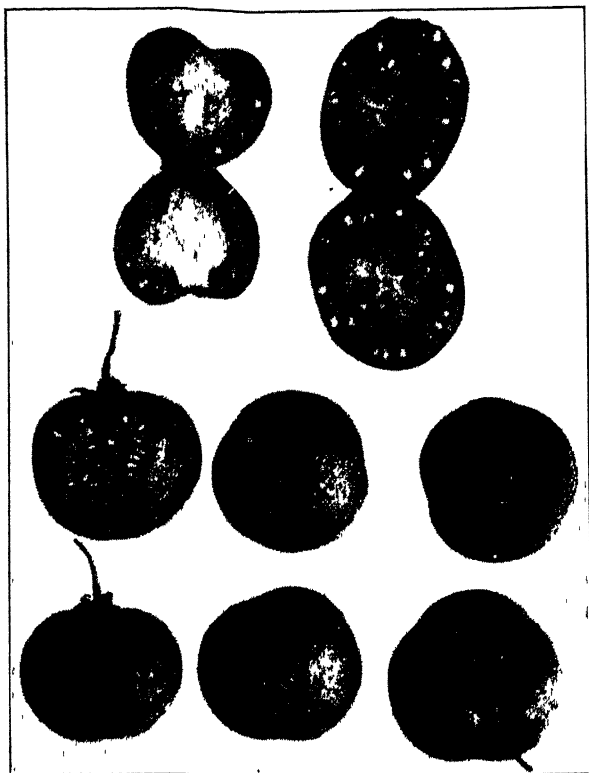


FIG. 60.—Potato seed balls and seed. (After F. A. Krantz.)

The young seedlings may be started in flats in the greenhouse the early part of March for latitudes such as Washington, D. C., by sowing the seed $\frac{1}{8}$ inch deep or thereabouts in a sandy loam. After four or five weeks the plants may be transplanted into pots or flats and taken to the field when conditions are favorable. Stuart believes it desirable to plant them 30 inches apart in the row.

Many seedlings must be tried and only a few will prove of value. The early history of seedling production indicates the importance of

sexual breeding. Results indicate that seedlings which produce tubers of irregular shape or with deep red or purple skin may well be discarded after the first year's trial. After another year's study those strains with undesirable characters such as low yielding ability, undesirable shape, deep eyes, unusual susceptibility to fungous diseases, and straggling or weak vine growth should be discarded and the few more promising types given a wide test to determine their adaptability and value under different conditions.

One of the greatest difficulties in potato breeding is the harmful effects and total loss which may result if the degeneracy diseases are present in the breeding plots. These diseases can be controlled from a practical standpoint by keeping the breeding stock well isolated from other potato fields and thus preventing primary infection.

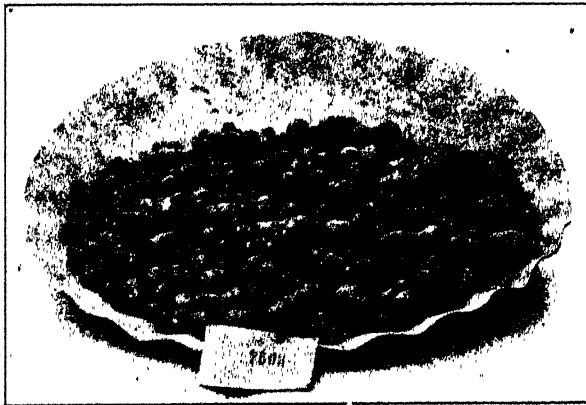


FIG. 61.—An unpromising first-year seedling. Crop of 1910. Note the large number of small, irregular shaped tubers. (After Stuart.)

Early Improvement through Seedling Production.—Probably no statement could be more illuminating than Stuart's discussion regarding early studies of potato improvement in the United States. The facts here related are taken from his publication.

During the period from 1840 to 1847 the wide occurrence of potato blight focussed the attention of potato growers upon the need of more resistant varieties. The Rev. C. E. Goodrich, of Utica, N. Y., believed this susceptibility to diseases was a result of long-continued asexual propagation. Through the agency of the American consul at Panama, South American varieties were introduced. Goodrich grew seedlings from Rough Purple Chili, one of the introduced varieties, and obtained a new variety which he named Garnet Chili which was introduced into the trade in 1857. Between 1849 and 1856 Goodrich raised a total of 8,400 seedlings. These experiments had considerable effect on the work of other breeders.

In 1861 Albert Bresee, of Hubbardton, Vt., grew a naturally fertilized seed ball produced by Garnet Chili. One of the seedlings produced was distributed under the name of Early Rose. The most careful breeder of this period was C. C. Pringle, of Charlotte, Vt., who selected varieties for crossing because of desirable characters. A variety by the name of Snowflake was one of the best known of his productions. Pringle, in the early 'seventies, contracted to produce potato seed for \$1,000 a pound.

Numerous varieties, probably resulting from naturally pollinated seed, were introduced by E. S. Brownell, of Essex Center, Vt. Among the better known of these were Brownell's Best, Beauty, Eureka, and Winner. The Early Ohio is another of the well-known varieties which

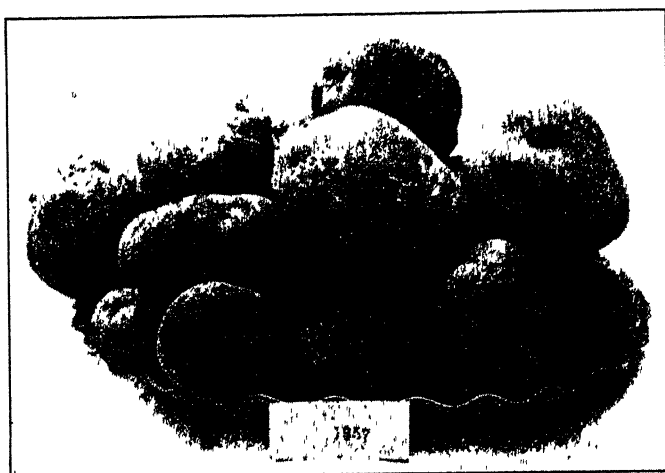


FIG. 62 —An extra-promising first-year seedling. Crop of 1910. 24 tubers. (After Stuart.)

were introduced about this time. It was obtained by Alfred Reese from a seedling of Early Rose and introduced in 1875. One of the first plant productions of note of the celebrated breeder, Luther Burbank, was obtained by growing seedlings of a potato ball which he found on an Early Rose vine in his mother's garden at Lancaster, Mass. Of 23 seedlings grown, one was of much promise. The new variety developed from this plant was introduced by Gregory in 1872 as Burbank's seedling. From naturally fertilized seed of Garnet Chili, E. L. Coy of West Hebron, N. Y., obtained a variety that was introduced in 1878 as Beauty of Hebron. These early experiments which produced some varieties that are still grown illustrate the marked effect which the introduction of a single variety may have on the production of new forms. Some of the varieties which resulted from the introduction and breeding experiments of the Rev. C. E. Goodrich are here listed:

TABLE LXXXI.--PEDIGREES OF SOME POTATO VARIETIES

Breeder	Variety used for seed	Seedlings named
Rev. C. E. Goodrich.	Rough Purple Chili	Garnet Chili
Albert Bresee.....	Garnet Chili	Early Rose
Alfred Reese.....	Early Rose	Early Ohio
Luther Burbank.....	Early Rose	Burbank
E. L. Coy.....	Garnet Chili	Beauty of Hebron

These early studies illustrate the general mode of production of new potato varieties which was carried on prior to 1900. At the present time the state experiment stations and the United States Department of Agriculture are taking a leading part in the production of improved varieties for the United States.

Clonal Selection.--The subject of bud mutations in potatoes is a somewhat difficult one, for there are numerous reported cases of such sudden changes. Many of the experiments were not performed with sufficient care to furnish acceptable evidence, although numerous apparently authentic cases of color changes have been reported. As an illustration of carefully controlled experiments those carried on by East (1910*a*) may be cited. In these studies each variety was started from a single hill. During the course of the study, five permanent changes from pink to white tubers, two permanent changes from long to round tubers, and four instances of changes from shallow to deep eyes were observed. On the basis of the modes of inheritance of these characters, the hypothesis was made that the changes resulted from the loss of dominant factors. Experiments in selection for high nitrogen content gave negative results. The statement was made:

It is true that all of the asexual variations have been losses of characters, while in sexual reproduction the formation of new characters occurs.

Dorst (1924) collected and examined as completely as possible all available cases of bud mutations. There seems to be little doubt of the authenticity of many of these cases. As reverse bud mutations from a new form to its original parent occur, Dorst does not believe that all sudden changes are the result of the loss of a dominant factor. While it is possible that desirable economic characters may have appeared occasionally as a result of bud mutations, the evidence for this belief is not very conclusive. Krantz (1924) has published considerable data recently which show that selection for yield or tuber form within a clone is futile. There is every reason to believe that sexual breeding is the promising mode of attack and in the production of improved new varieties bud mutation appears of comparatively little value. East quotes A. W. Sutton, who states:

I have no hesitation in affirming that there is no potato in commerce in England, and I might say in Europe, which owes its origin as a distinct potato to bud variation in any form whatever.

If this statement is true, it seems fair to conclude that there has been a somewhat loose usage of the term "bud mutation" in its application to raising the standard of a variety by any of the well-known methods such as tuber unit or hill selection (see Chap XXI). Accumulated evidence certainly points to the belief that the chief value of such work rests on the probable elimination of degenerate types. Evidence from Canada presented by Macoun (1918) is particularly illuminating. Four varieties, Early Rose, State of Maine, Empire State, and Delaware, were grown at the Experimental Farm at Ottawa, Canada, from 1890 to 1909, inclusive. The better tubers were selected from each year's crop and used to plant the following crop. Results are presented in Table LXXXII.

TABLE LXXXII—AVERAGE YIELD OF POTATOES OVER THE FIRST FOUR AND LAST FOUR YEARS OF A 16-YEAR PERIOD AND SUBSEQUENT YEARLY YIELDS OVER A FOUR-YEAR PERIOD

Variety	Year					
	1890-1893 bushels	1902-1905 bushels	1906 bushels	1907 bushels	1908 bushels	1909 bushels
Early Rose	257	317	150	128	69	18
State of Maine	325	361	132	174	97	62
Empire State	301	338	132	117	117	62
Delaware	296	352	103	114	156	53
Average..	295	342	129	133	110	49

For the 16-year period from 1890 to 1905, inclusive, the varieties were kept in a high state of productivity "due, no doubt, to careful selection and good cultivation each year." In 1906, however, there was a marked falling off in yield due to the unfavorable season. In the early part of the season there was sufficient rain but at about the time of the last cultivation, hot dry weather set in and continued throughout the season. During July there was also a severe attack of aphids. The vines, therefore, presented a stunted appearance and dried up early in the fall, the yield of tubers being very low. In 1907 and 1908 the seasons were also very unfavorable. The best tubers were again planted in 1909 and although the tubers used for planting presented a very favorable appearance, the yields were very low. A comparison was made in 1909 of tubers grown continuously at the Central Experiment Farm and newly

imported tubers grown under more favorable conditions. The yielding ability of the imported tubers in some cases exceeded that of the Central Farm tubers by as high as 500 per cent.

The rapid deterioration of varieties under certain conditions is a result, apparently, of degeneration diseases which have been referred to by various names some of which are "mild mosaic, leaf-rolling mosaic, rugose mosaic, leaf roll, spindling-tuber disease, and unmottled curly dwarf" (Schultz and Folsom, 1923, 1925). It has been shown that aphids are the principal agents in carrying these diseases of potatoes from plant to plant. The best means of control is the isolated seed plot and the use of healthy, disease-free stock.

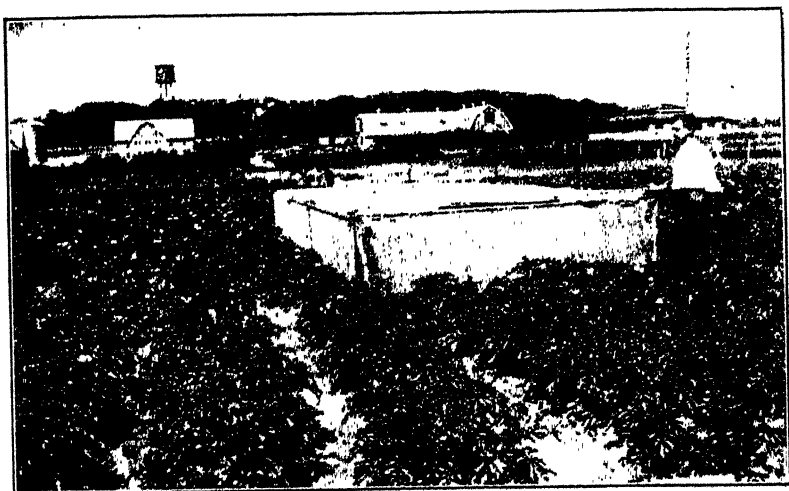


FIG. 63.—Tubers produced under such a cheesecloth cover have given good yields during the seasons 1918 and 1919 while tubers from uncovered vines produced very inferior yields. University Farm, St. Paul, Minnesota. (Courtesy of Krantz.)

Another explanation of degeneracy has been commonly mentioned. This is the hypothesis that continued asexual propagation causes senility or degeneracy. Perhaps this question may be answered for the potato by the consideration of a fact reported by Heribert Nilsson (1913). In a report of yields of 67 varieties, as tested in Sweden, he emphasized the fact that a variety, "Hvit Jämtlandspotatis," which has been cultivated more than 100 years proved to be the highest yielder. This is given as a refutation of the theory of senility.

It has not been the intention in this discussion to lead the practical breeder to discard "clonal selection" as one means of obtaining high yields, for it is a recognized fact that seed plot methods are of much practical importance. The results, however, are probably not due to the isolation of bud mutations but rather to the use of "disease-free" tubers

which have developed normally and which furnish the right conditions to give the resultant plants a favorable start.

Conclusion.—In general, clonal selection does not lead to the production of new varieties of great economic importance. Bud mutations have been observed although many of these are changes in color. Non-inherited changes of important tuber characters, such as shape, occur as a result of unfavorable environmental conditions. Degeneration diseases are a frequent cause of low yields and clonal selection, as a means of controlling these diseases, is an important phase of potato improvement.

Improved varieties may be obtained by sexual breeding as is well illustrated by the studies conducted in the United States during the last half of the nineteenth century. Sexual breeding has been used almost continuously in the European countries and in the early part of the present century more progress in this field was obtained in foreign countries than in the United States.

A knowledge of the mode of inheritance of important characters, particularly such characters as pollen sterility furnishes evidence which leads to the conclusion that further improvement through sexual breeding methods may be expected. The first step appears to be the production of desirable pollen parents through selection in self-fertilized lines. Suitable crosses can be made and the benefits to be obtained from the vigor of F_1 crosses can be retained in the potato because it is normally asexually propagated.

The breeding studies must be conducted in such a manner that degeneration diseases are controlled. This can be best accomplished by growing the breeding stock so that it is constantly isolated from potatoes infested with these diseases.

CHAPTER XIX

BREEDING OF VEGETABLES

INTRODUCTION

The long periods of cultivation and the various environments to which many of our vegetables have been subjected, have served to increase the number of varieties. Most of the vegetable varieties have been produced by commercial seed firms or by seed growers. An examination of any seed catalog shows numerous new forms which are being constantly introduced into cultivation. There has been a marked tendency among seeds men to give new trade names to old standard varieties. This has led to a great deal of confusion in nomenclature and much difficulty has been experienced in varietal identification. There is need of a more scientific test of varieties prior to introduction and of a standardization of varieties. Considerable progress has been made in classification of some vegetables. More information is needed regarding the mode of pollination and inheritance of special characters before methods of breeding can be intelligently applied. In this chapter the origin of both cross- and self-fertilized vegetables is briefly summarized. A discussion is given of methods of breeding for cross- and self-fertilized vegetables and the inheritance of certain characters is summarized.

Origin of Vegetables.¹—The ancient Greeks and Romans were familiar with some of our garden vegetables, on the other hand, many are of more recent origin and new varieties are being constantly introduced. The discovery of America introduced to civilization such important vegetables as the Irish potato, sweet corn, tomato, bean, sweet potato, pumpkin, squash, and pepper. Nearly all the other cultivated vegetables of temperate climate are indigenous to Europe or Asia.

Sweet corn, which is one of the most highly prized foods grown in America, is probably of recent origin. In Bailey's (1900) *Cyclopedia of American Agriculture*, Volume 2, page 402, the following statement occurs:

¹ For a complete history of the origin of vegetables see DE CANDOLLE, A., *Origin of Cultivated Plants*; Kegan, Paul, Trench & Co., London, Second Edition, 468 pages, 1886; HENSLOW, G., *The Origin and History of Our Garden Vegetables and Their Dietetic Values*, in *Jour. Roy. Hort. Soc.*, vols. 36 and 37, 1910-1911 and 1911-1912; STURTEVANT, E. L., *History of Garden Vegetables*, in *Am. Naturalist*, vols. 23, 24, and 25, 1889, 1890, and 1891.

The first sweet corn cultivated in America was derived from the Susequehanna Indians in 1779 by Captain Richard Beggall, who accompanied General Sullivan on his expedition to subdue the Six Nations.

How long *Zea mays saccharata* had been under cultivation is not known, but there is considerable evidence to substantiate the belief that at least the main types of corn, dent and flint, were cultivated a long time before the discovery of America.

Table LXXXIII taken from De Candolle (1886) presents a summary of the origin of some common vegetables.

TABLE LXXXIII—ORIGIN AND ANTIQUITY OF SOME VEGETABLES

Vegetable	Botanical name	Probable origin	Years cultivated
Asparagus .	<i>Asparagus officinalis</i>	Europe, west temperate Asia.	<i>B</i>
Bean, lima	<i>Phaseolus lunatus</i>	Brazil	<i>E</i>
Bean, common	<i>P vulgaris</i>	S Am found in Peruvian tombs	<i>E (?)</i>
Beet	<i>Beta vulgaris</i>	Canaries, Mediterranean basin,	<i>B</i>
	Tops as food	western temperate Asia.	
	Roots as food	A result of cultivation	<i>B</i>
Cabbage	<i>Brassica oleracea</i>	Europe	<i>A</i>
Carrot	<i>Daucus carota</i>	Europe, west temperate Asia (?)	<i>B</i>
Celery	<i>Apium graveolens</i>	Temperate and southern Europe, northern Africa, western Asia	<i>B</i>
Corn, sweet	<i>Zea mays var saccharata</i>		
Cucumber	<i>Cucumis sativus</i>	India.	<i>A</i>
Lettuce	<i>Lactuca sativa</i>	Southern Europe, northern Africa, western Asia	<i>B</i>
Muskmelon	<i>Cucumis melo</i>	India, Beluchistan, Guinea	<i>C</i>
Onion	<i>Allium cepa</i>	Persia, Afghanistan, Beluchistan, Palestine (?)	<i>A</i>
Parsnip	<i>Pastinaca sativa</i>	Central and southern Europe	<i>C</i>
Pea, garden	<i>Pisum sativum</i>	From the south of the Caucasus to Persia (?), northern India (?).	<i>B</i>
Pepper.	<i>Capsicum annuum</i>	Brazil (?)	<i>E</i>
Pumpkin	<i>Cucurbita pepo</i>	Temperate North America.	<i>E</i>
Radish	<i>Raphanus sativus</i>	Temperate Asia.	<i>B</i>
Salsify	<i>Tragopogon porrifolium</i>	Southeast of Europe, Algeria	<i>C (?)</i>
Spinach	<i>Spinacia oleracea</i>	Persia (?)	<i>C</i>
Sweet potato	<i>Convolvulus batatas</i>	Tropical America (where?).	<i>D</i>
Tomato	<i>Lycopersicon esculentum</i>	Peru.	<i>E</i>
Turnip	<i>Brassica rapa</i>	Europe, western Siberia (?)	<i>A</i>
Watermelon	<i>Citrullus vulgaris</i>	Tropical Africa.	<i>A</i>

A = Species cultivated more than 4,000 years.

B = Species cultivated more than 2,000 years.

C = Species cultivated less than 2,000 years

American species.

D = Cultivation ancient in America

E = Cultivation before discovery of America, but not showing signs of great antiquity.

Methods of Breeding Self-fertilized Vegetables.—Self-fertilized vegetables may be handled in the same general manner as other self-fertilized crops. Quality, yield, and disease resistance are the three most

important economic characters. Whether selection alone or hybridization followed by selection are to be used as a means of improving a crop is dependent upon the nature of the material. If the character combination is not present the only practical means of bringing it about is crossing followed by selection.

Disease resistance is of outstanding importance and resistant varieties have been obtained both by hybridization and selection.

Selection has been used by Edgerton (1918), of the Louisiana Agricultural Experiment Station, to isolate tomatoes resistant to wilt (*Fusarium lycopersici*). The improved technic followed is worthy of consideration. Seeds of a particular variety were planted in soil which had been sterilized previously and then inoculated with a pure culture of the wilt-producing organisms. When seedlings showed wilt infection they were pulled and discarded. Only plants which showed resistance were transplanted to the field. Tomatoes had grown continuously for eight or ten years on this field and it was known to be heavily infected with the wilt fungus. The use of this method permits a smaller acreage and insures the contact of each plant with the wilt organism. A selection made from a row of Acme grown in 1909 named "Louisiana Wilt-Resistant" was extremely wilt resistant but possessed other characters which made it undesirable for Louisiana conditions. Selections from the progeny of crosses between this form and Earliana showed considerable promise.

Durst (1918) reported the result of five years' selection for resistance to *Fusarium* of tomatoes. Varieties were found to differ a great deal in their resistance and unfortunately the most resistant ones produced poor fruit. After five years, some of the better strains stood up in soil which proved fatal to the original varieties. In addition to disease resistance, the selections also showed good yielding ability. Of 74 lots grown one year, the highest 14 yields were produced by selected strains.

Pritchard (1925) has made the interesting observation that tomato varieties resistant to wilt possess more than the average resistance to other diseases such as septoria blight, early blight, nail-head rust, and leaf mold.

Delwiche and Renard (1926) have noted that certain selections of canning peas are much more resistant to root-rot than others. After obtaining parental types of known qualities they can be improved by combining within a single variety the desirable characters of two or more varieties.

An interesting case of breeding beans resistant to physiological races of anthracnose has been given by Barrus, Burkholder, and McRostie. One of the most injurious diseases of the bean is anthracnose (*Colletotrichum lindemuthianum*).

Barrus (1918), as the result of an extensive study, was able to place beans in four groups with respect to susceptibility or resistance to this

disease Over two hundred varieties of beans commonly grown, besides many others, were tested. A considerable number of plants belonging to closely related genera were also examined. The cultures of anthracnose used for inoculating the varieties were obtained from widely separated geographical areas. By studying the reaction of the various cultures to each bean variety, two strains of anthracnose, alpha and beta, were discovered. With respect to their reaction to these two anthracnose strains, varieties of beans were placed in four groups.

- (ab) Varieties susceptible to both strain alpha and strain beta
- (aB) Varieties susceptible to strain alpha but resistant to strain beta.
- (Ab) Varieties susceptible to strain beta but resistant to strain alpha.
- (AB) Varieties showing some resistance to both strains

The most resistant variety of the last group is Wells Red Kidney. Results of crosses between varieties whose anthracnose reactions are known indicate that resistance to either the alpha or beta strain is inherited as a simple dominant, involving but a single factor difference (McRostie, 1919; Burkholder, 1918). It seems, therefore, very easy to produce resistant varieties to both strains by crossing and selection and thus to combine desirable economic characters and anthracnose resistance.

McRostie (1921) has published an interesting paper on further studies of disease resistance in common beans. The more extensive results obtained bear out the earlier views on the mode of inheritance of resistance to bean anthracnose. The studies carried out show that bean mosaic susceptibility is inherited. In F_1 there was a partial dominance of susceptibility over resistance and in F_2 a segregation which indicated a two factor hypothesis. In crosses between susceptible and resistant varieties in relation to the dry root rot, caused by the fungus, *Fusarium martii phaseoli* Burk., there was a dominance in F_1 of susceptibility and a segregation in F_2 that appeared to be on a 9:7 basis. In nearly all cases, resistant F_2 plants bred true to this character in F_3 . Results of this nature show the great practical importance of the application of Mendelian principles to breeding for disease resistance. It seems very likely that a large part of our most destructive plant diseases will be controlled eventually by the production of disease resistant varieties.

In breeding self-fertilized vegetables by the method of hybridization, it is necessary to grow the crop in such a manner that individual plants can be studied and observations on homozygosity obtained. Methods used will depend upon the nature of the crop. In the breeding of canning peas the crosses and selections from crosses are grown on woven wire supports until the lines appear homozygous (Delwiche and Renard, 1926). Standard sorts are grown as a means of estimating homozygosity of the new selections. In addition, the nursery remains in the same location

for several years so that there is a good opportunity for the elimination of strains with high disease susceptibility.

It has been observed by several workers that various types of "rogues" appear in cultures of peas. These off-types are of various kinds. Frequently the types have smaller, narrower leaves and pointed stipules. These types give only rogues the following generation. There are also intermediate types of rogues which do not breed true but give progeny consisting of rogues, intermediates, and non-rogues. Brotherton (1923, 1924) has reviewed the work of Bateson and Pellew. These workers found that the progenies of seeds from upper nodes contained fewer rogues than the progenies of seeds from the lower nodes. Brotherton offered a factorial explanation for the results he obtained in a study of rogues in the Gradus variety. The appearance of off types is assumed to be due to a mutation of a single factor x to X . In crosses between rogues and Gradus the F_2 generation consisted almost entirely of rogues, the Gradus type very rarely appearing. This result is explained by assuming that the heterozygous condition (Xx) is very unstable and that there is a marked tendency to mutate into the XX condition and hence at gametogenesis only an occasional x gamete is produced.

Delwiche and Renard (1926) have discussed various types of rogues which they observed. Later-blossoming, indeterminate-growing plants were observed among other types. They state that varieties differ widely in the percentage of rogues thrown and that rogues are most frequent in early varieties.

When mutations such as these occur, roguing is very important. Field roguing is considered the most desirable method of procedure by Delwiche and Renard.

INHERITANCE OF SOME CHARACTERS OF SELF-FERTILIZED VEGETABLES PEAS

Some Classification Characters.—Considerable historical interest attaches to the pea because of the fact that in studying the inheritance of certain characters in this plant Mendel discovered his now famous principles. Garden peas (*Pisum sativum*) are of two kinds, shelling and edible-pod. In the former, seeds only are used as food, while in the latter both pods and seeds may be so utilized. By far the greater part of the garden peas grown belong to the shelling group. Commercial varieties of garden peas are classified on the basis of habit of growth—climbing, half-dwarf, and dwarf; and length of time to mature—early, medium, and late. Peas of the early varieties may be round or wrinkled. Most of the medium and late maturing varieties belong to the sugar peas, which have wrinkled seeds when mature. Size of pod is another important classification character. Ripened pods may be inflated or somewhat constricted.

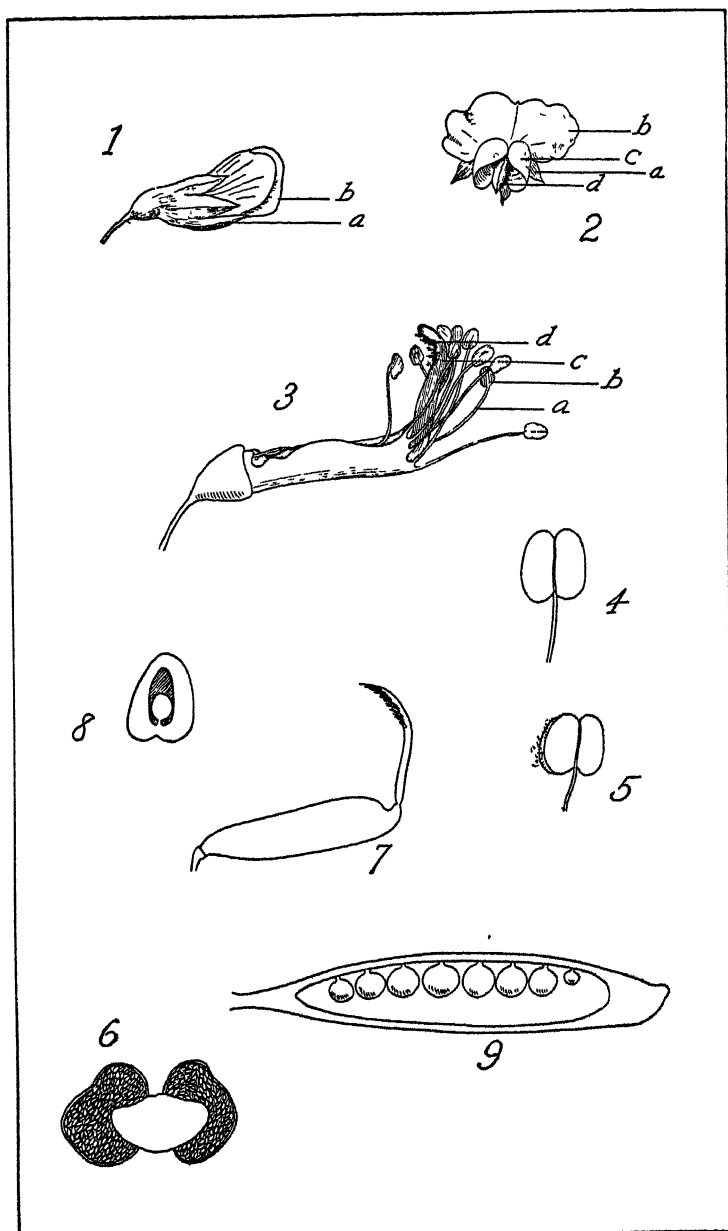


FIG. 64.—For description see opposite page.

Inheritance in Peas.¹—Peas have been subjected to rather extensive genetic analyses, hence more is known concerning inheritance in this vegetable than in most of the others. In general, the known facts regarding the manner of transmission of characters in peas is in accordance with the chromosome theory of inheritance.

Color.—There are a number of genes which influence the development of color and many of them interact in a somewhat complicated way. In Table LXXXIV are listed a number of genes together with a brief statement of their function.

TABLE LXXXIV.—IMPORTANT COLOR GENES IN PEAS

Gene	Function
<i>A</i>	Fundamental color factor
<i>A_r</i>	Reddening factor
<i>A_p</i>	Partial inhibitor of flower color
<i>B</i>	Bluing factor
<i>D</i>	Color in leaf axil (Allelomorphs <i>D^w</i> and <i>d</i>)
<i>P₁</i>	Color in pods
<i>H</i>	Orange seed coat
<i>M</i>	Brown marbling of seed coat
<i>F</i>	Purplish spotting on seed coat
<i>U</i>	Self-colored violet seed coat
<i>O_h</i>	Inhibitor of red seed coat
<i>Q</i>	Normal seed (<i>AQ</i> fundamental for seed-coat colors and indent seed)
<i>T_r</i>	Grayish black spots around "eye"
<i>M_p</i>	Partly inhibits effect of <i>qq</i>
<i>P_e</i>	Black "eye"

No attempt will be made here to discuss fully the interaction of the factors listed in Table LXXXIV. A few examples only are mentioned for purposes of illustration. For a more complete treatment the student is referred to the literature cited.

The fundamental color gene *A* alone produces light purple flowers, together with *D* or *D^w* a somewhat faint, reddish violet leaf-axil, together with *P₁* a violet pod, together with *Q* a brown or black "eye" with indent seed, together with *Q* and *O_h* a light brownish seed coat, together with *Q* and *F* a weak, violet spotting on the seed

¹ Summaries by WHITE (1917) and by WELLENSTEK (1925a) have been freely used in the following discussion.

FIG. 64.—Flower structure of pea.

1. A single flower—*a*, petals of calyx; *b*, side view of corolla.
 2. Front view of fully open flower—*a*, petal of calyx; *b*, standard; *c*, wing; *d*, keel.
 3. The sexual organs removed from the bud. (*Adapted from Muller.*) *a*, Filament; *b*, anther; *c*, style; *d*, stigma hairs.
 - 4, 5. Anthers.
 6. Cross section ovary.
 9. Longitudinal section ovary.
- Size: 1, $\frac{5}{4}n$; 2, $\frac{5}{6}n$; 3, greatly enlarged; 4, 5, $100n$; 6, greatly enlarged; 7, $8n$; 8, $40n$; 9, $40n$.

coat and together with *M* a brown marbling of the seed coat. The recessive allelomorph (*a*) of the *A* gene when in a homozygous condition produces white flowers, uncolored leaf axils, green or yellow pods, white or black "eyes" (never brown), practically uncolored seed coats, and non-indent seeds. The character "indent seed" should not be confused with wrinkled. The former is a seed coat, the latter an embryonic character.

Height—Mendel obtained monohybrid segregation with respect to height of plant. In a reciprocal cross of the varieties Autocrat and Bountiful, it has been suggested (Keeble and Pellew, 1910) that the inheritance of the character tallness involved two factor differences, one for length of internode and one for thickness of stem. On the other hand, White (1918) found height of plant dependent upon length and number of internodes. He explained his results on the basis of two genes for length and three for number of internodes. The results obtained by Tedin and Tedin (1923) in general corroborated those obtained by White.

Earliness.—The number of sterile nodes below the first flower influences earliness as has been pointed out by Wellensiek (1925*b*). Tedin and Tedin (1923) found one main factor and several modifiers for number of sterile nodes. Hoshino (1915) and Wellensiek (1925*b*) both explain the inheritance of earliness on a two-factor basis.

Bloom—Many strains of peas have a wax-like covering extending over nearly the entire surface of the stem and leaves. This glaucous condition is a dominant character and its inheritance is controlled by a single gene.

Fasciation is a recessive character that is apparently controlled by a single-factor difference.

Chlorophyll—Green foliage is dominant to yellow and apparently controlled by a single gene. At the Svalof Experiment Station, progenies of single plants have on several occasions produced 3 green:1 white seedlings (Tedin unpublished data).

Leaf Characters—Several leaf characters which give monohybrid segregation in F_2 have been reported. Reduced stipules (Pellew and Sverdrup, 1923), non-tendrilled leaves (White, 1917), dentate leaf margins (Wellensiek, 1925*a*), and grey spotting of the leaves (Tedin and Tedin, 1925) are each controlled in their inheritance by a single factor difference.

Keeled wings, an abnormal flower character reported by Pellew and Sverdrup (1923) owes its expression to a recessive gene.

Pod Characters.—Pods with a blunt apex are dominant to pods with an acute apex and their inheritance is best explained on the basis of a single-factor difference. Wellensiek (1925*b*) and White (1925) found normal, straight pods incompletely dominant over "upward curved" pods. The segregation obtained indicated monohybrid inheritance. The most thorough genetic analysis of the character "parchmented pod" is that made by Wellensiek (1925*b*). The results are explained on the basis of two factors, *P* and *V*. *P* alone produces a very thin parchment membrane but with *V* it produces a thick membrane. Vilmorin (1910) and Nohara (1918) obtained similar results. In the F_2 generation of certain crosses a ratio of 9 plants with parchmented pods:7 plants with non-parchmented pods was observed. Wellensiek (1925*c*) also made a genetic analysis of thickness of pod wall. The character thin wall was found dominant to thick wall and dependent for its expression on a single gene. The inheritance of pod color is best explained on a monofactorial basis with green dominant to yellow.

Seed Characters.—Mendel found yellow cotyledons dominant to green and dependent on a single factor difference for its expression. White (1917) reported a recessive yellow cotyledon color. Smooth seed (cotyledons with low water absorption capacity and simple oblong starch-grains) differs from wrinkled seed (cotyledons with high

water absorption capacity and round split starch grains) in one genetic factor with the former character dominant. The character known as "chenille" *i.e.*, the tendency for peas in the same pod to stick together, is recessive and monohybrid in its inheritance.

Linkage.—Evidence of linked inheritance in peas has been obtained by several investigators although to date there is but one linkage group which is known with certainty to contain more than two factors. Wellensiek obtained evidence that the genes *B* (purple flower color), *Cp* (straight pod), and *Bt* (Blunt pod apex) are linked and also that the genes *Cp* (green pod), *Cp*, and *N* (thin pod wall) are linked. These two groups were subjected to a three-point test and it was found that in both cases the results agreed very well with those which have been obtained in *Drosophila* and corn. Since the factor *Cp* is common to both linkage groups one would of course expect that all the factors are carried in the same chromosome. Certain other factors which are thought to be located in this chromosome have given rather puzzling results and more evidence is needed to clear up the matter. Kappert (1924) studied a hybrid which segregated with respect to ten character-pairs and found that only two pairs were inherited as if they were linked. Kappert attributes his results to a high percentage of crossing-over in peas. Hammarlund, whose investigation is reviewed by Wellensiek, in one instance found two factors that were closely linked and in another instance these same factors showed independent inheritance. On the whole it seems as if linkage relations in peas were somewhat complicated and much more evidence is needed before trustworthy conclusions may be reached.

BEANS

Some Classification Characters.—The species¹ of garden beans most commonly grown are *Phaseolus vulgaris* and *P. lunatus*. The former is divided, into snap and shell beans, although there is some overlapping in these groups. Shell beans are sometimes used as snap beans and *vice versa*. Time required to mature, habit of growth, whether climbing or bush, and size of plant are characters always described by commercial seedsmen. Length of bearing period is also an important character. Commercial growers sometimes desire varieties which may be harvested in a few pickings but for the home and general gardener, a variety with a longer bearing period is usually preferred. Size and shape of pod, number of seeds per pod in the case of snap beans, quality and color of the pod, are used in classification; with snap beans, stringless, fleshy, fine-grained pods are most desirable. The ease with which dry shell beans may be thrashed is of economic importance. In this group, color, size, and shape of seeds are usually included in varietal descriptions. Both productivity and disease resistance may differ strikingly in different varieties of beans.

¹ For a discussion of the classification of garden beans and a description of varieties see TRACY, W. W., American Varieties of Garden Beans, U. S. Dept. Agr., Bur. Plant Indust. *Bull.* 109, 173 pages, 1907; JARVIS, C. D., American Varieties of Beans, Cornell Agr. Exp. Sta. *Bull.* 260: 149-255: 1908.

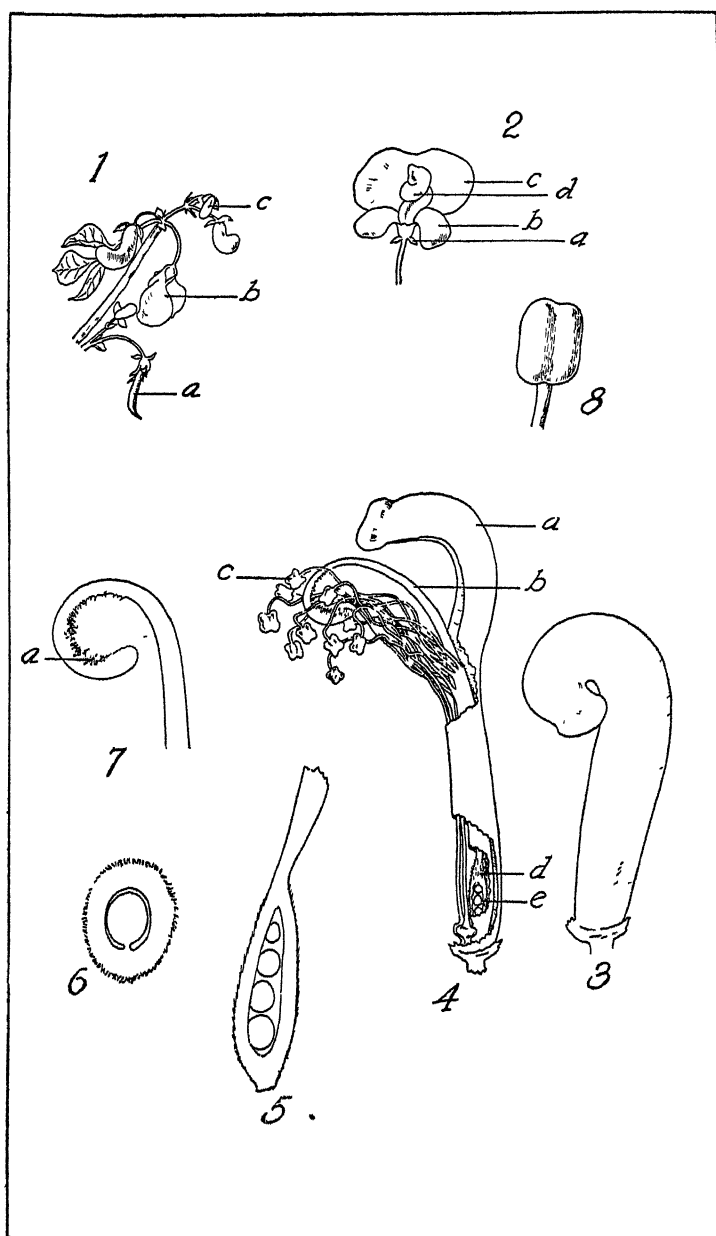


FIG. 65.—For description see opposite page.

Inheritance.—Genetic studies of the garden bean have been somewhat less extensive than those of the pea. Several investigations dealing with the inheritance of color, size characters, and disease resistance have been reported.

Seed Coat.—Seed-coat color has been shown by Shaw and Norton (1918) to involve several factor differences. The work was carried on with 21 varieties including more than 40,000 plants. Crosses between mottled and self-colored varieties yielded mottled beans in F_1 and showed 3:1 ratios in F_2 . Mottled \times white varieties gave mottled in F_1 , and in F_2 the ratio of 9 mottled:3 self-colored:4 white usually resulted. It was demonstrated that pigment patterns and pigment colors were controlled by distinct factors. All plants with white or eyed beans bore white flowers while plants with mottled or self-colored beans usually bore pink flowers.

More recently, Sirks (1922) has investigated the inheritance of seed-coat color in *P. vulgaris* and *P. multiflorus*. Light mottling was found recessive to black mottling and also to solid black. White behaved as a recessive character. In some cases, segregation obtained with respect to color was simple and in other cases more complex. On the basis of his own and other work, Sax makes the following factorial explanation of seed-coat inheritance.

P is necessary for pigmentation

T, an extension factor for total pigmentation, the recessive of which results in a partially pigmented or eye bean

Y and *Z* are factors in the same chromosome which together result in mottling. *Y* and *Z* may also exist separately in non-mottled beans and, when brought together in crosses, give mottled beans which seldom, if ever, become homozygous for mottling.

Other factors control type of mottling and color of pigmentation.

Height.—The inheritance of stature in beans, as in peas, is in some crosses dependent on a single factor difference while in other crosses several factor differences are involved. Emerson (1916) has explained the result of crossing a tall-pole (indeterminate growth) bean and a short bush (determinate growth) bean or a short pole bean and a tall bush bean, by a three-factor hypothesis. The following values to be added to an initial value of three internodes were assigned to the factors: Factor *A* either homozygous or heterozygous added ten internodes approximately, while factors *B* and *C* each added two internodes when homozygous and one when heterozygous. Results were explained factorially as follows:

Parent 1..... *AABBCC* = 17 internodes or *AAbbcc* = 13 internodes

Parent 2..... *aabbcc* = 3 internodes or *aaBBCC* = 7 internodes

F_1 *AaBbCc* = 15 internodes or *AaBbCc* = 15 internodes

Many new forms would naturally be produced in F_2 .

FIG. 65.—Flower structure of bean.

1. Small branch showing—*a*, developing pod; *b*, *c*, flowers in different stages of development.

2. Front view of fully opened flower—*a*, calyx; *b*, wing; *c*, standard; *d*, keel.

3. Enlarged keel.

4. Keel with outer part broken away to show—*b*, style; *c*, anther; *d*, undeveloped pod; *e*, ovary.

5, 6. Longitudinal and cross section of pod.

7. Enlarged stigma showing—*a*, stigma hairs.

8. Anther.

Size: 1, n ; 2, about $2n$; 3 to 8, greatly enlarged.

Flowers, Pods and Seeds.—Tschermak (1916) has brought together and summarized the data on the inheritance of economic characters in the garden bean Table LXXXV is made up from his summary

TABLE LXXXV —INHERITANCE IN THE BEAN

Contrasted characters	F_1 condition	F_2 behavior
Colored \times white (flowers)	Colored	3 1
Green \times yellow (unripe pods)	Green	3 1
Non-constricted \times constricted (pods)	Non-constricted	3 1
Round \times flat (pods)	Round	3 1
"Non-stringiness" \times "stringy" (pods).	Intermediate or approaching non-stringiness	Stringy pods recessive (1 out of 4)
Blunt \times sharp (pod ends)	Approaches blunt	Approaches 3 1
Broad \times narrow (pods)	Approaches broad	Segregation irregular
Long \times short (pods)	Approaches long	Segregation irregular
Cylindrical \times spherical (seeds)	Approaches cylindrical	Segregation irregular with spherical seeds constant.
Cylindrical \times kidney-shaped (seeds)	Approaches cylindrical	Segregation irregular with kidney-shaped seeds constant
Yellow \times green (cotyledons)	Yellow (apparent on crossed seed)	3 1 (segregation apparent on F_1 plants)

Linkage.—The number of diploid chromosomes in *P. vulgaris* and *P. lunatus*, as determined by Karpechenko (1925), is twenty-two. Some interesting cases of linkage between seed-coat colors and size of seed have been reported by Sax (1923, 1924). In a cross between Improved Yellow Eye and Small White, the F_2 generation showed simple 3:1 ratios for pigmented *vs.* white, mottled *vs.* self-colored, and completely pigmented *vs.* partially pigmented or eyed. The white segregates were lighter in weight on the average than the pigmented segregates, thus indicating that some of the differences in average seed weight are dependent on size factors inherited in a simple Mendelian manner. The discovery of this linkage relationship is of considerable importance as it shows that a quantitative character may be inherited in the same way as a qualitative character.

TOMATO

Classification.—The tomato belongs to the genus *Lycopersicum*, of which there are several cultivated species. Tomatoes are classified on the basis of vine habit, either standard or dwarf, leaf type, period of maturity, size and color of fruits, and other characters. As a result of breeding experiments, many different combinations of characters have been made. A classification of tomatoes based on the inheritance of fruit shape has been suggested by Warren (1923). As a result of crossing several varieties two complimentary factors governing depth and two other complimentary factors governing non-fasciation of fruits were discovered.

Inheritance.—Price and Drinkard (1908) were among the first investigators to report on the simple Mendelian behavior of certain

tomato characters. Several genetic studies of this important vegetable have been made since, some of which are mentioned below.

Miscellaneous Characters.—Table LXXXVI, taken from similar ones compiled by Tschermak (1916) and Jones (1917), presents a brief summary of inheritance in the tomato. Fruit shape is dependent on several factors according to Crane (1915), Groth (1912, 1915), and others. Some of the foliage characters are also somewhat complicated in their inheritance (Groth 1911). The inheritance of each of the other characters listed in the table is dependent on single factor differences, the F_2 segregation ratio being 3:1.

Heterosis in the F_1 generation of certain tomato crosses and its commercial possibilities for increased production have been pointed out by Wellington (1912), Hayes and Jones (1916), Frimmel (1925), and others. Groth, of the New Jersey State College Experiment Station, made a study of size inheritance in the tomato fruit. The results are explained by what the author (1914) terms "Golden mean." If a and b represent the respective magnitudes or volumes of size characters of the parents, the F_1 is represented by \sqrt{ab} rather than $(a + b)/2$. This hypothesis was put forward as non-Mendelian and in explanation of results in size inheritance frequently attributed to multiple factors. Emerson (1914b) has shown that the hypothesis is essentially based on multiple factors. The studies of Frimmel (1922) and Myers (1924) also indicate that the inheritance of size of fruit in the tomato is somewhat complicated.

TABLE LXXXVI.—INHERITANCE OF CHARACTERS IN THE TOMATO

Characters	Dominant	Recessive
Fruit shape.....	Spherical	Pear-shaped
Fruit shape.....	Roundish conical	Roundish compressed
Loculation of ovary.....	Two-loculed	Many-loculed
Endocarp color.....	Red	Yellow
Epicarp color.....	Yellow	Colorless
Fruit surface.....	Smooth	Pubescent
Leaf margin.....	Serrate (normal or fine leaf)	Entire (potato or coarse leaf)
Leaf type.....	<i>Pimpinellifolium</i> type	<i>Esulentum</i> type
Leaf color.....	Green	Yellow
Inflorescence type.....	Simple	Compound
Vine habit and leaf surface.....	Standard, smooth	Dwarf, rugose
Height of plant.....	Tall or normal	

Linkage.—The diploid number of chromosomes in the tomato is 24 and therefore one would expect to find not more than 12 linkage groups. Lesley and Mann (1925) have reported two cases of triploidy. The plants appeared normal with the exception of a tendency toward gigantism. The fruit of the triploids were small and contained few seed.

It has been pointed out by Jones (1917) that the data of Hedrick and Booth (1907) and Price and Drinkard (1908) show linkage relations between the factors for vine habit and fruit shape and also between those for leaf color and loculation of ovary.

An interesting case of linkage between the inheritance of color and size of fruit has been studied by Lindstrom (1926). There are two main factor pairs which govern fruit color in tomatoes, *Rr* and *Yy*. The dominant *R* factor produces red flesh and the recessive *r* yellow flesh. The dominant *Y* produces yellow pigment in the epidermal cells and the recessive gene *y* gives a colorless condition in these cells. These two factor pairs are inherited independently but the *Yy* factor pair is closely linked with size of fruit. The relationship is shown in Table LXXXVII, taken from Lindstrom.

TABLE LXXXVII.—LINKAGE BETWEEN THE INHERITANCE OF SIZE AND COLOR OF EPIDERMIS OF FRUIT IN THE TOMATO

Name	Skin color				Differences
	Yellow (<i>Y</i>)		Colorless (<i>y</i>)		
	N	Average weight, grams	N	Average weight, grams	
Red cherry (<i>RRYY</i>). Golden Beauty (<i>yy</i>) <i>F</i> ₂ generation ... <i>F</i> ₁ × Golden Beauty	75 33	7 3 ± 0 3 . 23 6 ± 0 6 51 2 ± 2 0	21 27	166 5 ± 6 4 38 3 ± 2 1 79.2 ± 2 8	14 7 ± 2 2 28 0 ± 3 4

The average weight of the fruit of the *F*₁ generation of the cross was 23.9 ± 0.4 grams which indicated a partial dominance of small fruit. Both the *F*₂ generation and the backcross with the Golden Beauty parent show a marked association between the *y* genes and relatively large fruit.

Evidence is also given which indicated that possibly there was some linkage between the inheritance of fruit size and the *Rr* factor pair.

PEPPERS

Classification Characters and Inheritance.—Garden peppers which are commonly grown for pickles or for condiments belong to the species *Capsicum annuum*. From the standpoint of their utilization as food, peppers may be divided roughly into two groups—hot and mild, depending on flavor. Mild peppers are frequently used green for slicing or stuffing, whereas hot peppers more often serve as a condiment in spice mixtures. Number of days to mature is usually given by seedsmen in describing varieties. Color, size, shape, and uniformity of fruit are other important commercial characters.

A limited number of inheritance studies with this vegetable have been made. Webber (1911) and Ikeno (1913) report the behavior of certain characters in the second generation after a cross. Below is given a tabular summary of a part of the results obtained.

TABLE LXXXVIII.—INHERITANCE IN THE PEPPER

Contrasted characters	F_1 condition	F_2 behavior
Violet × white (flower)....	Violet (considerable variation in amount of violet coloring)	3:1
Violet flower associated with violet coloring in leaf-stem and ripe fruit.		
White flower associated with green leaf and stem except for a dark spot near attachment of petiole.		
Umbel × non-umbel (inflorescence)...	Non-umbel	3:1
Red × orange (ripe fruit).....	Red	3:1
Pubescence × non-pubescence (stems and leaves)	Less hairy than hairy parent	15 pubescent:1 non-pubescent
Pungent × sweet (fruit) ...	Pungent	Approx. 3:1

In the inheritance of size of leaf, Webber obtained results which clearly indicated that several factor differences were involved and a like result was obtained by both Webber and Ikeno with regard to size of fruit. The character of the peduncle, whether erect or recurved, was found by Ikeno to be dependent on a single factor difference, erect being the recessive condition when the fruit had ripened. During the flowering stage and early development of the fruit the heterozygous individuals for this character-pair showed dominance for the erect peduncle.

CROSS-FERTILIZED VEGETABLES

Cross-fertilized vegetables may be roughly divided into three main divisions:

1. Those which are normally cross-pollinated but which set seed freely on selfing and show little or no evidence of sterility.

2. Those which are wholly or partially self sterile.

3. Those which are cross-fertilized owing to the dioecious condition.

Much more study of the mode of pollination of vegetables is necessary before it is possible accurately to classify vegetables according to their mode of reproduction. Illustrations are given here of breeding methods and results obtained for the different groups.

Some Illustrations of Methods and Results of Breeding.—The breeding of cabbage resistant to yellows (*Fusarium conglutinans* Wollenw.) at the Wisconsin Experiment Station (Jones and Gilman, 1915) is of great economic importance. Less than a decade ago, truck farmers in certain sections of Wisconsin were so discouraged from the ravages of yellows that they were about to abandon cabbage growing. The method of producing resistant cabbage strains may be briefly summarized. It had been noticed that there were usually a few plants which escaped the disease in a field where nearly all plants were badly infected with the organism. These apparently resistant plants were selected on the basis

of type. After storing over winter, all that were of the same general type were planted together and were far enough removed from any other similar planting to insure against contamination by foreign pollen. Selfed seed was not obtained but most plants not bagged set seed abundantly. Some plants were eliminated because of low seed production. Progeny of the retained plants were grown separately and their resistance to yellows was tested. In this way several strains of cabbage highly resistant to yellows have been produced. Further studies have been reported and numerous resistant varieties have been produced (Jones *et al.*, 1920). The writers emphasize the fact that resistance is not absolute and that environmental factors influence very markedly the development of the disease. They state, however:

By following the proper methods any skilful cabbage grower who has *Fusarium* sick soil may either undertake with reasonable confidence to develop a resistant strain of his own, or having secured one of these resistant strains he can maintain its resistance and produce his own seed.

Mass selection is often used in breeding beets. Only those roots which come up to an adopted standard are stored over winter and set out the following spring to become the seed-producing plants. Carrots and parsnips, when bred by mass selection, are handled in a similar manner. Although varieties of any one of the crops, beets, carrots, or parsnips, freely intercross, there is no crossing between the three different kinds of vegetables (Malte and Macoun, 1915). This fact may be utilized in making planting plans.

Line or family breeding has been used also in the improvement of this class of crops. In this method, progenies of individual plants are studied and pollination is controlled partially by planting material of a similar nature in the same plot.

Breeding sugar beets by controlled pollination was begun at Svalöf, Sweden, in 1914, and the first really successful isolations were harvested in 1916 (Nilsson, 1922, 1923).¹

The percentage of lines breeding true for morphological characters or only segregating in one character after the first selfing was about 45. In general, the selfed lines gave a somewhat lower yield than the standard sorts, although a number of them proved to be as high yielding after five generations of selfing as the best of the normally pollinated varieties. In many hundreds of investigated beet and mangel strains, less than 5 per cent showed signs of so-called degeneration. Fertility was inherited and strains with high self-fertility produced larger and better developed seeds than partially self-sterile strains.

Each botanical species of the *Cucurbitaceae* constitutes a freely intercrossing group of varieties. The flowering habit encourages cross-

¹ From summaries made by G. NILSSON-LEISSNER.

fertilization. In spite of these facts the authors believe that in some cases progress may be made by breeding methods recommended for self-fertilized crops or more specifically for crops which yield ample seed on selfing. When such a plan is adopted for naturally cross-fertilized crops

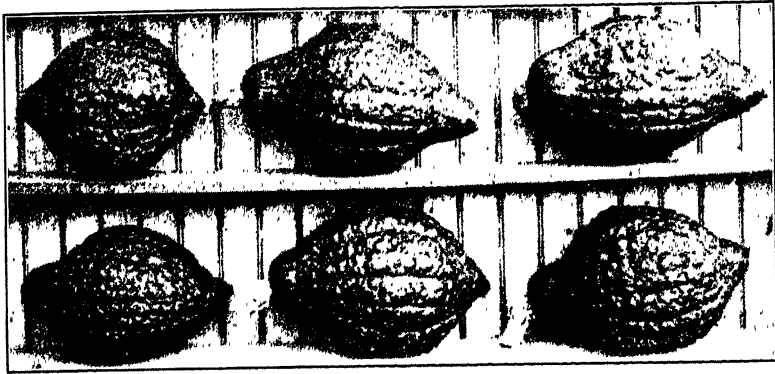


FIG. 66.—A strain of Hubbard squash isolated by self-fertilization which is comparatively uniform for the production of large fruits of uniform shape. Minnesota Exp. Sta. (Courtesy of Bushnell.)

it becomes necessary to insure selfing by artificial means. By reducing ordinary varieties to pure lines, a much more exhaustive study of the material at hand may be made, and on the basis of this study desirable combinations obtained by hybridization or pure lines of commercial value may be isolated. The method which is adopted after the isolation

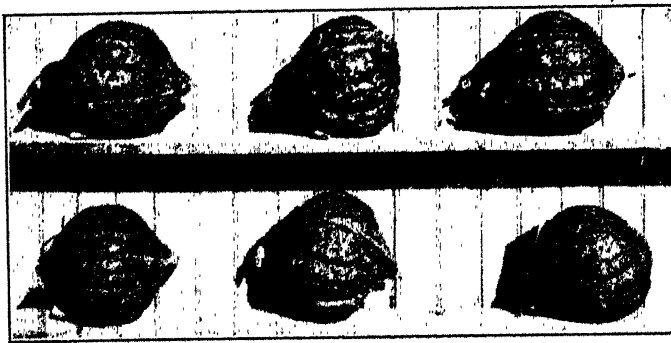


FIG. 67.—A small fruited strain isolated from a commercial variety of Hubbard squash by self-fertilization. Minnesota Exp. Sta. (Courtesy of Bushnell.)

of homozygous lines through self-fertilization will depend on the degree in which vigor is lost as a result of selfing. Relatively homozygous lines have been isolated in squashes by Bushnell (1922) of the Minnesota station, and by Sinnott and Durham (1922) of the Connecticut Experiment Station. Some lines which are comparatively uniform appear

vigorous while others are less vigorous. Types for markedly different characters which are relatively uniform have been isolated.

In some cases, varietal crosses have been used as a means of producing improved sorts. One of the most serious handicaps to the production of watermelons in the Southern States is the presence of wilt, due to an organism, *Fusarium niveum*. "Citron" or "stock melon," so-called locally, is a non-edible variety of *Citrullus vulgaris* resistant to wilt.orton (1911) conceived the idea of crossing this form with edible forms. He hybridized Eden, a good quality melon, with citron. The F_1 was very vigorous and of intermediate type. Between 3,000 and 4,000 F_2 plants were grown and 10 fruits selected on the basis of resistance and quality. After selecting the resultant progeny for several years the variety Conqueror was isolated. It is disease resistant, has a tough rind, and does not sunburn easily. The flesh is juicy and of good quality, although not equal to the finest. These studies were made in South Carolina. It was found that Conqueror retained its resistance when grown in Iowa but seemed to lose it when grown in Oregon, on the Pacific coast. It is possible that there are physiological forms of this disease similar to what have been found for other diseases. If such is the case the differences in susceptibility under the two conditions would result from the presence of different physiological forms of the pathogene.

Asparagus (*Asparagus officinalis*) is dioecious in habit of flowering although hermaphrodite plants have been discovered (Norton, 1911-1912). With this vegetable, cross-pollination is usually necessary for seed production.

The fungus, *Puccinia asparagi*, has occasioned a great deal of alarm among commercial asparagus growers, particularly those of the eastern United States. This rust differs from that occurring on the small grains in that all stages of the rust occur on the asparagus plant. At the invitation of Massachusetts growers, the United States Department of Agriculture, in cooperation with the Massachusetts Agricultural Experiment Station, undertook to produce a resistant variety. Norton (1911-1912, 1913) has reported on this investigation. Because of the dioecious habit of asparagus it was necessary to select two kinds of plants—male and female. Selections were based on rust resistance, *i.e.*, only plants which showed a high degree of resistance were chosen. In 1909 the first test of the transmission of relative rust resistance was made. Twelve lots saved from as many plants showing various degrees of rust resistance were planted in duplicate in short rows. After the young shoots appeared they were dusted several times with fresh uredospores. Later in the season observations were made on the degree of infection. The results are given in Table LXXXIX (Norton, 1913).

Table LXXXIX shows clearly that rust resistance is inherited. Various artificial crosses were made between forms showing rust resist-

ance. The progeny of some of these crosses proved highly resistant and in some cases were more resistant than the parents. By this method several strains of asparagus with a high degree of resistance have been produced. In the production of a new form a male plant obtained in 1910 from a lot of New American of unknown origin proved of marked ability in transmitting vigor and rust resistance to the progeny. The female plants known as Mary and Martha were selected from the variety

TABLE LXXXIX.—TRANSMISSION OF RUST RESISTANCE IN ASPARAGUS

Row	Source of seed	Type of plant	Rank seedlings in resistance		
			First lot	Second lot	Average
1	A1-6	Badly rusted, near rusty bed . . .	7	9	8.0
2	A3-61	Very resistant female	6	5	5.5
3	A4-7	Resistance good	3	7	5.0
4	A4-17	Resistance fair	10	8	9.0
5	A7-5	Resistance good	4	3	3.5
6	A7-15	Resistance good	2	4	3.0
7	A7-25	Resistance good	5	2	3.5
8	B24-27	Very rusty	11	10	10.5
9	B24-28	Very rusty	9	11	10.0
10	Old field	Rusty	12	12	12.0
11	Old field	Resistant	8	6	7.0
12	Frank Wheeler old bed	Best resistant female	1	1	1.0

Reading Giant. Two or three other females have been selected and the crossed seed obtained from these selected plants has been distributed under the name Washington asparagus (Norton, 1919). Some of these strains are now being offered for sale by commercial seedsmen.

Norton suggests the following method for breeding asparagus: after two mated plants have proved their value by the progeny test, they should be dug up and propagated by crown division. These clones are isolated together and retained exclusively as breeding stock. Isolation may be accomplished by a fine-meshed cage to prevent the entrance of bees or by planting at a safe distance from other beds of asparagus. Producing seed in a greenhouse by hand pollination also has been found successful.

Spinach, like asparagus, is dicecious but, unlike asparagus, staminate and pistillate plants do not occur in approximately equal numbers (Zwann, 1925). In addition to staminate and pistillate plants, hermaphrodites also occur. One strain was observed producing as high as 98 per cent staminate plants. Climatic conditions seem to influence the

relative frequency of occurrence of staminate plants. A strain has been isolated by Zwann which is apparently a pure hermaphrodite.

As a result of crossing Manchuria with Savoy, a new variety (Virginia Savoy) of spinach which is resistant to mosaic has been produced (Smith, 1920, 1921; Geise, 1924). In addition to disease resistance this new variety possesses desirable market qualities.

INHERITANCE OF CHARACTERS IN CROSS-POLLINATED PLANTS RADISH

Origin, Inheritance, and Breeding.—The cultivated radish, *Raphanus sativus*, was grown by the ancient Greeks and Romans. There has been considerable discussion as to its origin. Some writers have thought that the cultivated form with its fleshy root arose directly from *R. raphanistrum*. This belief was apparently substantiated by experiments in which the wild form was grown under cultivation and after several years cultivated radishes were obtained. Rielle (1914) tested this hypothesis by a controlled experiment. The wild form was grown under cultivation and self-fertilized. Three years of selection failed to produce roots which resembled the fleshy roots of *R. sativus*. On the other hand, when the wild and cultivated forms were both grown on the same plot and seed was saved from the wild form, it was found to be an easy matter, after three years' selection, to obtain roots which resembled the fleshy roots of *R. sativus*. These results were believed to be due to natural crossing of the wild and cultivated forms. This hypothesis was tested by making an artificial cross. Segregation for root condition occurred in F_2 . This led Rielle to conclude that former experiments in which cultivated radishes were obtained from the wild through selection were best explained through natural crossing.

A successful cross was made between *R. sativus* ♀ and *Brassica oleracea* ♂ by Karpechenko (1924). The F_1 generation bred *inter se* as well as back-crossed with each parent proved wholly sterile. Mitosis apparently took place in a normal manner but at meiosis the chromosomes failed to pair and were distributed at random to either pole.

R. sativus roots contain sugar while wild roots contain no sugar. F_1 crosses contain less sugar than the cultivated forms. The presence of starch in the root of the wild radish, particularly in the bark, is a character which separates it from the cultivated varieties. This proved a dominant in crosses. Cultivated radishes show various color intensities. Color is apparently inherited in much the same manner as in other crops. Individual radish plants were grown under cover by Rielle and self-fertilized seed was produced in abundance. This led Rielle to suggest that homozygous strains be first produced. These would then furnish material for accurate inheritance studies as well as be of much value for economic breeding purposes. On the other hand, Stout (1920) has stated that there is considerable self-sterility in the cultivated radish. Up to the present, mass selection has been most frequently used as a means of breeding radishes (Tschermak, 1916).

BEETS¹

Both garden beets and sugar beets belong to the species *Beta vulgaris*. Kajanus (1913) made a study of the inheritance of root forms in mangels and sugar beets.

¹ In a recent monograph, Vilmorin (1923) has presented the results of a study of the origin, history, classification, and genetics of the cultivated beets with particular reference to the sugar beet. For a detailed study the student is referred to this monograph.

In general, the F_1 roots were intermediate between the parental forms. Sugar beet crosses in which wedge-shaped forms were involved proved to be exceptions. Wedge-shape was completely dominant over walnut-form and also over long, somewhat slender roots (post-shape). The other beet shapes studied were oval and round. Most of the ratios obtained in F_2 could be satisfactorily explained on the basis of four factors—two involving length of root and two concerned with form.

CULTIVATED VEGETABLES OF THE GENUS BRASSICA

Cabbage and several other vegetables such as cauliflower, brussels sprouts, kohlrabi, and rutabagas, belong to the genus *Brassica*. Few inheritance studies have been made with this group of vegetables. Cabbage has received more attention from a breeding standpoint than the others.

Tschermak (1916) maintains that many of the kinds of vegetables belonging to the cabbage group freely intercross when in close proximity at blooming time. A few *Brassica* crosses have been reported by Ragionieri (1920). Vigorous first-generation hybrids were obtained from crosses between white turnip, *B. rapa*, and Chinese cabbage, *B. chinensis* var. Pe-tsai. On the other hand, crosses between the latter and some of the other *Brassicaceae* set no seed.

Price (1911-1912) and Jones and Gilman (1915) were not able to produce self-fertilized seed under a bag. Tschermak (1916) maintains that many of the kinds of vegetables belonging to the cabbage group freely intercross when in close proximity at blooming time. The above facts are fundamental and show the method of breeding which must be used. They may also aid in explaining some unusual inheritance results.

Price crossed varieties of crinkled-leaf and smooth-leaf cabbage, obtaining dominance for crinkled leaf in F_1 with no segregation of this character in F_2 , i.e., all plants (419) had crinkled leaves. With respect to size, shape, and solidity of heads, color of foliage, and length and thickness of stem, considerable more variability was obtained in F_2 than in F_1 . The segregation among the progeny of a natural hybrid observed by Kristofferson (1921) indicated dihybrid inheritance with respect to color of midrib, but more complex inheritance with respect to other characters. In some cases transgressive segregation was obtained. Some strains of cabbage when sown in late July or early August will produce good solid heads the following spring; on the other hand, certain strains when grown under similar conditions will flower and not produce heads. Evidence was obtained by Sutton (1924) which indicated that the tendency to form seed the second year was inherited as a simple recessive character. In a cross between a crinkled-leaf cabbage and a cauliflower, Price observed that the thick, leathery leaf of the latter was dominant in F_1 and was the only apparent leaf characteristic in F_2 . Head cabbage crossed with headless cabbage produced nothing but headed forms both in the F_1 and F_2 generations. As to type of head, the cabbage or leafy form was found to be dominant over the type of head of the cauliflower. In F_2 the cabbage head form was maintained without apparent segregation. Crosses between cabbage and brussels sprouts gave F_1 and F_2 generations identical with respect to habit of growth, i.e., all were determinate. Axillary buds were more common in the hybrids than in ordinary cabbage. The thick stem of kohlrabi was found to be dominant in a kohlrabi-cabbage cross and a limited number of F_2 individuals showed no segregation of this character.

Sutton (1908) crossed reciprocally kohlrabi and Drumhead cabbage, obtaining, in F_2 , 3 non-kohlrabi plants: 1 resembling kohlrabi. The parental forms did not appear in the F_2 generation. Drumhead cabbage crossed with thousand-headed kale produced 204 plants in F_2 . Of these, 176 resembled a dwarf type of thousand-headed

kale with leaves broader than usual and fewer branches, 26 resembled cabbage, and 2 plants were much like brussels sprouts

The difficulty of a study of inheritance in the *Brassica* genus arises from the heterozygous condition of many forms and the self-sterile condition. Before the results are accepted as examples of non-Mendelian behavior, a critical study in which all facts are considered should be made. In cabbage there is apparently a complicated inheritance. The above results are satisfactorily explained on a multiple-factor hypothesis. In crossing heterozygous forms, the F_1 generation may be as variable as the F_2 generation. In the inheritance of any particular character, the number of factor differences may be so large as to make the appearance of parental forms improbable in a small F_2 generation.

ECONOMIC CUCURBITACEÆ

Introduction and Classification.—The family *Cucurbitaceæ* is of considerable historical interest. Sageret (1826) and Naudin (1856, 1859a, 1859b), two pre-Mendelian workers, made extensive hybridization

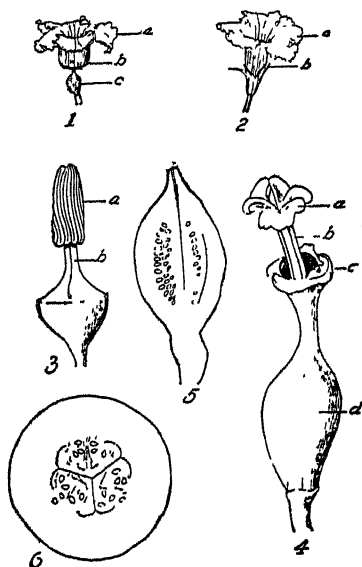


FIG. 68.—Structure of flowers of squash.

1. Female flower—*a*, corolla; *b*, calyx; *c*, fruit.
 2. Male flower
 3. Male flower with calyx and corolla removed.
 4. Female flower with calyx and corolla removed showing— *a*, stigma; *b*, style; *c*, point of attachment of calyx and corolla; *d*, undeveloped fruit.
 - 5, 6. Longitudinal and cross sections of fruit.
- Size: 1, 2, $\frac{1}{4}n$; 3, 4, $\frac{1}{2}n$.

studies with some species belonging to this family and Naudin made a species classification on the basis of genetic behavior which is accepted at the present time. All the forms which cross readily were placed in the same species group.

Cucumis sativus—Cucumber

Cucumis melo—Muskmelon, cantaloupe

Cucurbita pepo—Pumpkin, gourd, summer squash, and varieties of winter squash. Peduncle hard and ridged.

Cucurbita maxima—Large field squash and winter squash. Peduncle soft and fleshy.

Cucurbita moschata—Squash. Little grown in United States. Peduncle much enlarged where attached to fruit.

Citrullus vulgaris—Watermelon, citron.

Cummings (1904) experienced no great difficulty in crossing Golden Custard (♀) with Crookneck (♂), varieties of squashes belonging to *C. pepo*. The reciprocal cross proved difficult, only five out of 284 pollinations producing fruit with viable seed. A histological examination revealed the fact that the male generative nucleus of Custard penetrated the ovary of Crookneck and took up a position which, in many cases, was in close proximity to the egg cell but for some reason fusion did not occur in most cases.

Bailey (1890), as the result of many artificial pollinations, concludes "that the field pumpkins and the summer and fall types of bush squashes (*C. pepo*) do not cross with the running squashes of the Hubbard, Marblehead, Boston Marrow, turban, and mammoth types (*C. maxima*).” In the *Cyclopedia of American Horticulture*, Bailey (1900) states that *C. moschata* and *C. pepo* may be crossed artificially but it is doubtful if they cross naturally. *Cucurbitaceæ* in general are monœcious and largely dependent on insects for pollination.

The diploid numbers of chromosomes for several species of *Cucurbitaceæ* have been reported by Kozhukhov (1924–1925). The number was found to be 14 in *Cucumis sativus*; 22 in *Citrullus vulgaris*; 24 in two varieties of *Cucumis melo*; 40 in two varieties and 42 in one variety of *Cucurbita pepo*; and 48 in each *Cucurbita maxima* and *C. moschata*.

Immediate Effect of Pollination.—There is a popular belief widely disseminated that pumpkins and watermelons should not be grown in close proximity because of the immediate effect of cross-pollination. A similar belief exists with regard to cucumbers and muskmelons. Evidence accumulated by various plant breeders shows that this idea is not founded on fact. The work of Bailey at Cornell and Pammel at Iowa may be cited. The former (1890) was unable to find any immediate effect of cross-pollination between varieties of *C. pepo* and likewise between varieties of *C. maxima*. Bailey not only was unable to demonstrate any immediate effect of pollen in varieties which could be crossed but he was even unable to produce crosses between cucumbers and muskmelons. Ninety-seven flowers of several varieties of melons were pollinated with different varieties of cucumbers. Not a single fruit set. Twenty-five reciprocal pollinations were also made. One fruit developed but pro-

duced no seed. The setting of parthenocarpic fruit without fertilization is not an infrequent occurrence in cucumbers. Pammel (1892), in an intermingled planting of varieties of each of the following species, *Citrullus vulgaris*, *Cucumis melo*, *Cucurbita maxima*, *Cucumis sativus*, and *Cucurbita pepo* provided excellent facilities for inter-specific pollinations. Neither the watermelons nor the muskmelons showed contamination. Some hand pollinations between species were made, but no cross-fertilization was obtained.

More recent investigations by Becker (1922) and Vavilov (1925) verify the conclusions reached by Bailey and Pammel.

The variability in flavor of commercial varieties of melons is undoubtedly partly responsible for the erroneous belief that they may be contaminated by other species of cucurbits growing in close proximity. At the Connecticut Station an extensive varietal test was made. Most of the varieties were of very inferior quality even though they were exposed only to muskmelon pollen. Even if crossing occurred, there is no conclusive evidence that xenia would result.

CUCUMBER

Wellington, (1913) studied the inheritance of the following characters: color, size, number of spines, smooth or rough skin, and obtained ratios indicating monohybrid segregation. Smooth skin and small spines, few in number, appear to be linked. Heterosis shown by increased number or size of fruit, has been observed in the F_1 of certain cucumber crosses (Hayes and Jones, 1916). The F_1 of a cross (Reeves, 1918) between American type (20 per cent parthenocarpic) and English type (normally parthenocarpic) showed 20 per cent parthenocarpic.

A comparison of a few American, German, Dutch, and French varieties of cucumbers with respect to their relative resistance to bacterial wilt was made by Doolittle (1922). The foreign varieties proved much more susceptible, an average of over 90 per cent of the plants being attacked, whereas an average of approximately 30 per cent of the American varieties were attacked.

MUSKMELON

Lumsden (1914), of the New Hampshire Agricultural Experiment Station, has made rather extensive studies of inheritance in the muskmelon. The tabular statement on p. 349 gives a summary of his work.

These data show that all the characters studied segregated in the second generation. There is some indication that the contrasted characters in color of skin, size of seed, size of fruit, and form of fruit are each separated by a single main factor difference. In a cross between varieties producing round and elliptical fruits, respectively, the F_1 fruit was recorded as round, while the F_2 gave the ratio of 2.76 round: 1 elliptical. The other two characters, netting and ribbing, indicate more complex inheritance. *Delices de la table* (σ^7) has deep ribbing and no netting; Sutton's Superlative (φ) has no ribbing and pronounced netting. The F_2 generation showed a variation of from 5 to 100 per cent with respect to each character.

TABLE XC.—INHERITANCE IN THE MUSKMELON IN A CROSS BETWEEN THE VARIETIES SUTTON'S SUPERLATIVE AND DELICES DE LA TABLE

Characters	No. of F_1 plants	F_1	No. of F_2 plants	F_2 ratio
Color of skin..... Yellow \times green.....	.. 1 Yellow	.. 79	Yellow: green 2.76: 1
Form of fruit..... Round \times elliptical.....	.. 1 Round	.. 79	Round: elliptical 2.76: 1
Ribbing..... Ribbed \times non-ribbed.....	.. 1 Ribbed	.. 79	5-45 46-100 per cent per cent ribbing: ribbing 1: 1.82
Netting..... Netted \times smooth.....	.. 1 Netted	.. 79	5-45 46-100 per cent per cent Netting: netting 1: 1.63
Size of seed..... Large \times small.....	.. 1 Large	.. 79	Large: small 2.95: 1
Size of fruit..... Large \times small.....	.. 1 Large	.. 79	Large: small 2.59: 1

SQUASHES AND GOURDS

Emerson (1910), while at the Nebraska Experiment Station, made a study of size inheritance in a cross between Yellow Crookneck and White Scallop summer squashes. He found that length of neck and diameter of bowl were intermediate between the parents in F_1 . The second generation showed a complete series of dimensions and shapes from one parent to the other. The same investigator crossed Striped Spoon gourd with Filipino Horned gourd. Results similar to those of the squash cross were obtained.

The inheritance of several characters of *Cucurbita Pepo* has been studied by Sinnott (1922) and Sinnott and Durham (1922). White color of fruit was found dominant over yellow and yellow over green. The evidence indicated that there were two separate factors for white, a factor for yellow recessive to white and dominant over green, and a recessive factor for green. A single factor difference was found between solid color and striping, with the former appearing in some cases as a dominant and in other cases as a recessive. In surface of fruit, wartiness was found dominant over smoothness and produced by at least two independent genes cumulative in their effect. The inheritance of "disc" shape (dominant) of fruit *versus* "sphere" (recessive) was found dependent on one main factor difference although one or more modifying factors may produce minor changes. Flesh color, too, seemed to be comparatively simple in its inheritance. Other characters were investigated and found to be definitely inherited but the exact manner of their inheritance was not determined.

CHAPTER XX

FRUIT BREEDING

The improvement of fruit crops offers an interesting field of study for the trained investigator. Many fruits are in a complex heterozygous condition. For this reason, and because fruits are propagated by asexual methods, Mendel's law does not have here the same value as for the breeder of self-fertilized crops. There are also many fruit crops which are totally self-sterile so that cross-pollination, either natural or artificial, is essential to the production of fruit. Unlike an annual crop the individual fruit tree often takes many years to grow before fruiting. For these reasons, methods of handling are often of much greater importance than methods of breeding. It is, therefore, of utmost importance that the student first make an intensive study of the botanical relatives, methods of culture, varieties, and environmental necessities of the crop before undertaking breeding operations.

ORIGIN AND ANTIQUITY OF SOME FRUITS¹

Wild fruits without doubt played an important rôle in the food supply of primitive man. As the art of agriculture came to be developed because of the necessity of obtaining enough food to supply the increasing human population, the fruit crops were gradually introduced into cultivation. Some of our most prized fruits, as the apple, grape, and plum, have been cultivated since earliest times; while others, as the strawberry, black raspberry, and blackberry, have been brought under cultivation since America was discovered.

The wild species from which our fruits have been developed may still be found today. Wild plums may be found in nearly every state of the United States, while in central and northern Asia the wild relatives of apples, pears, apricots, cherries, and plums are of frequent occurrence.

The wild crabs are found in abundance, in both the Eastern and the Western Hemispheres. As the cultivated European varieties gave good results when introduced into the United States, the breeding of apples has not been seriously undertaken until comparatively recent times. The cultivated varieties are very numerous. Our pears were developed from two very different wild species, *Pyrus communis*, the wild pear of western Asia and Europe, and the hard, gritty sand pear of northern

¹ A paper by WHITE (1916) has been used freely in this discussion.

China. *P. communis* is the source of our eating pears, such as the Bartlett, while interspecific crosses furnished our cooking and winter pears.

Peaches were first developed in China. When one compares the little hard, bitter wild peach of China and our cultivated varieties the results of early breeding are strikingly illustrated.

There are three groups which are commonly accepted as the ancestral forms of our cultivated plums: (1) The thorny wild European species which produces dark purple fruits about the size of a pea. These are the source of our prune varieties. (2) North American native wild plums which have a very juicy flesh without much meat. Several species are recognized (Wight, 1915). (3) A Chinese-Japanese wild species. Many of the cultivated varieties of plums are largely of hybrid origin.

TABLE XCI.—ORIGIN, PROBABLE LENGTH OF TIME OF CULTIVATION, AND COMMENTS ON SOME CULTIVATED FRUITS (*after White, 1916*)

Name	Date	Origin	Remarks
Apple.....	A	E. Europe, W. Asia	Very different type common to China.
Apricot.....	A	Central Asia, China	Wild species variable.
Blackberry.....	F	United States	Wild species very variable.
Blueberry.....	F	E. and N. North America	Four species, often confused with huckleberry.
Cranberry.....	F	E. and N. North America	Cultivated for about 100 years.
Currant, red.....	C	Northern Hemisphere	White and yellow varieties are forms.
Cherry, sour.....	B	Asia Minor, S.E. Europe (?)	
Cherry, sweet.....	B	S. Europe, E. Asia	
Grape, Old World.....	A	West temperate Asia	California and Old World grape.
Grape, New World.....	F	North America	Many probably hybrids.
Gooseberry.....	C	N. Europe, N. Africa, W. Asia, United States	Old and New World species distinct.
Grapefruit.....	B	Malayan and Pacific Islands east of Java	Largely cultivated in United States.
Lemon.....	B	India	
Orange, sweet.....	C	India	Numerous hybrids with other species.
Peach.....	A	China	Hundreds of varieties.
Pear.....	A	Temperate Europe and Asia, N. China	Two species and hybrids between them.
Plum.....	A	S. Europe, W. Asia, N. America	Much hybridized group.
Raspberry, red.....	C	N. Europe, Asia, N. America	Varieties and hybrids of two species.
Raspberry, black.....	F	Middle North America	
Strawberry.....	F	Temperate N. America, Pacific Coast of N. and S. America, Europe	At least three species involved.

A, cultivated for more than 4,000 years.

B, cultivated for more than 2,000 years.

C, cultivated for less than 2,000 years in the Old World.

F, cultivated since the discovery of America. Often only very recently.

There are over 120 wild species of cherries which are native to Asia and from 200 to 1,500 wild species of raspberries and blackberries. The

variation in type of the wild red raspberries of New England is a good illustration of a wide diversity of forms. Some of these are probably results of crosses with escaped cultivated varieties. Natural hybridization certainly played a large part in the evolution of such fruits and the selection of promising wild seedlings furnished the major part of our cultivated varieties.

Fletcher (1916) has described 1,879 varieties of strawberries which originated in North America and 26 European varieties which have attained prominence in this country. The strawberry is largely a hybrid product of four or more species.

The citrus fruits are all of Asiatic origin. Present cultivated varieties have for the most part been produced during the last 100 years. The grapefruit industry of the United States has been developed in the last 25 years. This fruit, which is a native of islands lying to the south of Asia, was introduced into the West Indies early in the eighteenth century and more recently from the West Indies into Florida. Table XCI, which is part of a table published by White (1916), is a summary statement of the source and the length of time under cultivation of some of our most highly prized fruit crops.

The mode of origin of some of the better United States fruit varieties has been compiled by Dorsey (1916) from the New York Agricultural Experiment Station fruit monographs. A summary statement is presented in Table XCII.

TABLE XCII.—ORIGIN OF VARIETIES OF APPLE, CHERRY, PLUM, PEACH AND GRAPE

Fruit	Both parents known	One parent known	Neither parent known	Origin as bud sports	Total
Apple	3	39	588	4	634
Cherry	20	61	1,064	0	1,145
Grape	74	57	72	0	203
Plum	49	108	524	1	682
Peach	2	13	69	1	85
Total.	148	278	2,317	6	2,749

These data show that nearly 85 per cent of the commercial fruit varieties of apple, cherry, plum, and grape have been obtained by selecting promising chance seedlings, that one parent was known for a little more than 10 per cent of the varieties described, while only a little over 5 per cent of the commercial varieties originated from crosses in which both parents were known. Only six out of 2,749 varieties are known to have originated as bud sports.

SOME EARLY STUDIES IN FRUIT IMPROVEMENT¹

The preceding discussion gives some idea of the great number of varieties of our fruit crops. While many of these are from chance seedlings, a considerable percentage resulted from definite attempts to produce improved forms.

Von Mons.—One of the earliest horticulturists was a Belgian by the name of Von Mons, who was born in 1765 and died in 1842. He was a chemist but followed horticulture as an avocation. His studies were carried out for the purpose of proving the truth of certain philosophical theories. While he did not succeed in substantiating the theories, his work was of considerable value to horticultural science and practice. His most important studies were with pears. In 1823 there were 80,000 seedlings in his nursery. About this time he issued a catalog in which 1,050 pears were described by name or number. Of these, 405 varieties were of his own production. His practice was to sow, select, and resow, and, without doubt, a part of his great accomplishments was a direct result of cumulative selection.

Knight.—Thomas Andrew Knight has already been mentioned as a man who contributed much to the art of plant breeding. He was born in England in 1759 and died in 1838. A part of his work was carried on with such fruit crops as apples, pears, and peaches. He emphasized the value of crossing as a means of producing improved forms for he believed this method was more rapid than Von Mons' selection practice.

American Pomology.—Throughout the nineteenth century American pomologists made great progress in the improvement of fruits. While many American named varieties occurred as chance seedlings, others were the result of careful breeding. The strawberry and grape are examples of fruits in which many of the varieties are a result of controlled breeding. Selection and crossing both played important parts in the improvement of varieties. Hovey was one of the best known of the early strawberry breeders who worked during the first half of the nineteenth century.

The production of improved American varieties of grapes well illustrates a common method of the production of new fruits. Old World grapes did not succeed in the greater part of the United States, as European varieties proved very susceptible to diseases, particularly mildew. The production of American varieties from native wild species gave us many of the cultivated types. Some of the best of the early varieties arose as chance seedlings. Concord was thus discovered by Ephraim W. Bull and introduced about 1853. It has been frequently used as a parent for the production of the improved forms. Some improved forms

¹ For an account of the evolution of American fruits the reader is referred to BAILEY, 1898; MUNSON, 1906.

have resulted from crosses between native and European varieties, Delaware being generally thought to have been so produced.

With the plum, as with the grape, the native American species have furnished the source from which a large part of the American varieties have been produced (Wight, 1915). Several wild species have been used and frequently the varieties which have proved best adapted to a given locality have been produced from the wild form which is native to the same region.

SOME CONSIDERATIONS OF FRUIT BREEDING

Fundamental laws of heredity furnish the same foundation for a development of correct breeding technic in the fruits as with other crops. There are, however, some factors which modify breeding methods. For example, a single tree takes up considerable field space and thus has a greater value than a single plant of wheat or corn. In comparing varieties and clonal lines, the question of soil heterogeneity must be considered for this is probably a frequent cause for the variation in yield from different trees of the same variety when grown in the same orchard. Self-sterility, which is so prevalent among fruit crops, often prevents the production of homozygous material; while the use of heterozygous material does not allow the breeder to make systematic crosses with a knowledge of the genetic constitution of the parents. In spite of these difficulties which the fruit breeder must face, there has been a consistent attempt to use fundamental breeding principles and, at present, methods are becoming somewhat standardized. The advantage which comes to the breeder from the fact that an improved variety may be propagated asexually and need not be reduced to a homozygous condition, tends to offset other difficulties. Some of the more general problems will be here illustrated.

Overcoming Soil Heterogeneity.—Batchelor and Reed (1918) have made an interesting study of variability in orchard plots. They used orange, lemon, walnut, and apple trees in the investigation. From 224 to 1,000 trees of each of the different fruits were studied and the coefficient of variability for yield of single trees determined. The coefficient of variability of the clonal varieties ranged from 29.72 to 41.23 per cent. Thirty-five per cent might be considered a fair average. Multiplying this by 0.6745 gives 23.6, the probable error in percentage of the mean.

The effect on the coefficient of variability of increasing the number of trees in a plot was studied; a comparison of plots containing 1, 2, 4, 8, 16, and 24 trees being made. Table XCIII gives an average of tests with oranges, lemons, apples, and walnuts. The results are based on a study of more than 2,000 individual trees.

TABLE XCIII.—EFFECT OF INCREASING THE NUMBER OF TREES PER PLOT

Number of trees per plot	Average coefficient of variability	Average reduction of coefficient of variability by increasing number of adjacent trees per plot	
		Increase from	Average reduction
1	37.78 ± 0.52		
2	30.89 ± 0.55	1 to 2	6.89 ± 0.76
4	26.76 ± 0.62	2 to 4	4.13 ± 0.83
8	24.27 ± 0.77	4 to 8	2.49 ± 0.99
16	22.58 ± 1.01	8 to 16	1.69 ± 1.27
24	19.74 ± 1.08	16 to 24	2.84 ± 1.48

From these results the conclusion is reached that eight trees is about the correct number which should be used in a plot.

The question of replication, *i.e.*, the systematic distribution of plots over the field, is taken up. Results computed for four- and eight-tree units are given for oranges, apples, walnuts, and lemons. Table XCIV gives an average of data from these crops.

TABLE XCIV.—EFFECT OF REPLICATION IN FOUR- AND EIGHT-PLOT UNITS

Four trees in a unit	Eight trees in a unit	Number of systematically replicated plots
26.76 ± 0.60	24.27 ± 0.77	1
15.12 ± 0.47	12.84 ± 0.56	2
13.58 ± 0.53	11.27 ± 0.63	3
9.29 ± 0.40	9.54 ± 0.57	4
8.40 ± 0.40	7.95 ± 0.49	5
8.49 ± 0.49	6

The conclusion seems warranted that four systematically replicated plots greatly reduce the error which arises from soil heterogeneity. The data also show that four systematically distributed plots of four trees each are somewhat more reliable than two plots of eight trees each.

As was presented in Chap. IV, Harris has given a reliable means of estimating soil heterogeneity by the correlation between the neighboring plots of a field. The test was applied to an orange grove which appeared to have uniform soil conditions. The correlation between the yield of eight-tree plots as ultimate units and grouped combinations of four such adjacent plots was found to be $r = +0.533 \pm 0.085$. This showed a pronounced heterogeneity in the soil of this orchard. However, the correlation computed between the yield of an eight-tree ultimate unit and the yield of the combination of four such systematically distributed units was not much larger than the probable error.

These facts show the unreliability of yields of single trees as a criterion of productivity, that eight-tree plots give much more reliable results, and

that plot replication is of as much value in studies of fruit-yield as of farm crops. Where quality is a major criterion, single trees give fairly reliable information.

The several factors which caused variability in a certain Ben Davis orchard were determined by Sax and Gowen (1923). It was found that 62 per cent of the total variability was owing to environmental factors other than soil, 18 per cent to soil, and about 15 per cent to factors which cause permanence of yield, such as grafting stocks, bud mutation, and unknown factors.

Self-sterility and Heterozygosity.—One of the chief difficulties of systematizing methods of work is due to the heterozygous condition of most fruit material. A commercial variety may be extremely valuable and yet be heterozygous for many characters. On the other hand, the commercial variety may be homozygous for a large part of its characters. It seems reasonable to conclude that the more nearly homozygous the parental variety, other things being equal, the greater value it would have as a parent.

The ability of impressing its characteristics upon the larger part of its offspring has been called prepotency by animal breeders. Such prepotency is genetically explained by the supposition that the prepotent parent is homozygous for certain dominant factors for the characters under observation. Hedrick and Wellington (1912) showed that some crosses between apple varieties produced a considerable percentage of individuals with small fruits. Thus the cross between Ralls and Northern Spy gave great variability in size of apples, while the cross between Sutton and Northern Spy gave progeny in which no trees were obtained which produced small fruit. One of the great difficulties is that it takes several years to learn the varieties which, when crossed, will give certain desired combination.

TABLE XCV.—INCREASE IN WEIGHT OF SEED AND FRUIT DUE TO CROSS-POLLINATION

Pollination	Average weight of seed, grams	Average weight of fruit, grams
Newtown × self	0 05	73
Newtown × Bellflower.	0 40	104
Newtown × Spitzenberg.	0.66	147
Newtown × Jonathan	0 65	162
Newtown × Grimes Golden	0.60	173
Spitzenberg × self	0 13	100
Spitzenberg × Newtown.	0 65	126
Spitzenberg × Arkansas Blk.	0.68	128
Spitzenberg × Jonathan	0.70	144
Spitzenberg × Baldwin	0 71	157

Another difficulty which must be considered is that many varieties of fruits are self-sterile. This is of utmost importance in commercial fruit production for it is necessary to interplant such a variety with some variety which produces an abundance of pollen which is capable of fertilizing the variety in question and which blooms at about the same period. The self-sterile habit likewise prohibits the reduction of the material to a homozygous condition. Frequently self-fertile varieties give great increases in weight of seed and fruits as a result of cross-pollination. Therefore, pollinators, varieties which have proved desirable as pollen parents, are often of considerable commercial value in increasing yield in the case of self-fertile varieties.

Table XCV gives two typical cases taken from the work of Lewis and Vincent (1909) with the apple.

The large increases in weight of seed as a result of crossing are very noticeable. Increases in size of fruit are also of much importance.

TABLE XCVI.—CONDENSED STATEMENT OF NUMBER OF SELF-FERTILE, SELF-STERILE, AND PARTIALLY SELF-FERTILE VARIETIES OF FRUIT CROPS

Fruit	Number self-fertile	Number self-sterile	Number partially self-sterile	Authority	Remarks
Grape.....	7	13	5	Dorsey, 1914 after Beach (1898, 1899)	Self-fertile and partially self-fertile have upright stamens and pollen with germ pore. Self-sterile varieties have reflexed stamens and pollen with no germ pore.
Grape.....	Beach, 1902	Pollen of self-sterile varieties can not fertilize other self-sterile varieties.
Plum	All cultivated varieties of native American species except New Ulm and Robinson are self-sterile.			Dorsey, 1919	Results given by Dorsey are from studies of Waugh (1896, 1897, 1898, 1899, 1900, 1901), Goff (1894, 1901), and Waite (1905).
Plum.....	18	10	5	Sutton, 1918	All self-sterile varieties set fruit when pollinated with any other variety with few exceptions.
Cherries.....	3	17	2	Sutton, 1918	
Apples.....	8	16	10	Sutton, 1918	
Apples.....	28	59	..	Lewis and Vincent, 1909	From 50 to 200 pollinations were made for each variety. If no seed set, variety is classed as self-sterile. All varieties with some seed setting are classed as self-fertile, although some are partially self-sterile.
Pears.....	Bartlett and Kieffer pears are self-sterile.			Fletcher, 1911	

For the commercial grower or the fruit breeder, it is essential to know which varieties are self-sterile. In order to illustrate the conditions

generally found regarding sterility, a compilation of some results is presented in Table XCVI. Citations to literature are given so that the reader may go to the original sources when he desires to know what category any particular variety belongs to.

The causes of sterility have been determined in some cases. In the strawberry it is due to at least two causes (Valleau, 1918):

1. The dioecious condition
2. The production of aborted pollen grains or microspores in otherwise normal anthers.

In the grape, Dorsey (1914) has found sterility to be associated with both hybridity and the dioecious condition. The varieties which produce reflexed stamens seldom produce fertile pollen. Dorsey states:

Sterility has been found to be due to the pollen rather than in the pistil. Sterile pollen in the grape results from degeneration processes in the generative nucleus or arrested development previous to mitosis in the microspore nucleus.

Pollen abortion occurs both in pure and hybrid forms but is not considered a cause of lack of fertility as abundant pollen is produced in the grape.

In the plum, pollen abortion is not as a rule the cause of self-sterility. The outstanding features as given by Dorsey (1919) are:

- (a) A constancy of expression of self-sterility even in *P. domestica* in which about one-half of the varieties are self-fertile; (b) the occurrence of cross-sterility; and, (c) the slow growth of pollen tubes under the condition of self- and cross-sterility.

This type of sterility is comparable with that in the tobacco crosses previously discussed, where sterility resulted from slow pollen-tube growth. In this case the pollen tube growing from the pollen grain into the tissues of the style never reaches the embryo sac. The self-sterile condition is believed by Dorsey to be a dominant character in the plum and to be inherited, segregation into sterile and fertile forms occurring at reduction division. Knight (1917) has made a study of self-sterility in the apple and the conclusions reached show the manifold causes which must be considered in a study of the problem. For this reason the conclusions are here given verbatim.

1. Self-sterility in Rome Beauty is not due to sterility of the pollen as has been shown to be the case in certain varieties of grapes.
2. Sensitiveness of pollen to over-abundant moisture supply is not involved here as a factor, as has been shown by Jost for the pollen of many grasses, barley especially; and by J. N. Martin for the pollen of red clover. The pollen of Rome Beauty and many other varieties germinated in distilled water.
3. Rome Beauty stigmatic fluid extracts offer no inhibition to the germination and growth of Rome Beauty pollen.
4. Rome Beauty stigmas offer no particular mechanical obstruction to the penetration of Rome Beauty pollen tubes.

5. Self-sterility of Rome Beauty is not due to inability of its own pollen tubes to grow deep enough to reach the egg. This has been suggested as the cause of self-sterility in certain pear and apple varieties by the work of Osterwalder.

6. From present indications one important factor in self-sterility of Rome Beauty is the relatively slow rate of growth of Rome Beauty tubes in Rome Beauty stylar tissue. Doubtless other factors will be found upon further examination.

Inheritance of Some Characters.—The mode of inheritance of most fruit characters has as yet not been determined. There are, however, numerous experiments under way for the purpose of learning how individual characters behave in crosses. The lack of information in this field is due to the heterozygous condition of many fruit varieties and to the fact that with many fruit crops so long a period elapses between the time of sowing the seed and the production of fruit.

Apple.—Inheritance in the apple is well illustrated by a study made at the Geneva Station by Hedrick and Wellington (1912). Crosses were made in 1898 and 1899 and 148 seedlings were grown. In 1912, 106 of the seedlings had come into bearing. These 106 seedlings resulted from 11 crosses. The first generation naturally does not furnish very reliable data as a means of deciding the mode of inheritance of individual characters.

Three types of skin color were studied, red, yellow, and intermediates. The conclusion was reached that Ben Davis and Jonathan were both pure for red color of skin, as crosses between these varieties gave seedlings which produced fruit with a red skin. Other crosses led to the belief that yellow is recessive and that a cross between red and yellow is intermediate in skin color. Sweetness was believed to be a recessive character to acidity with the indication that the F_1 was intermediate.

Similar results were obtained by Auchter (1921) at the Maryland Experiment Station. In a cross between Tolman and a dwarf form of *Malus torringo*, Crandall (1920) found that the F_1 seedlings strongly resembled the male parent in appearance of tree except that they were not dwarf. The fruit did not resemble either parent. It is stated that the outstanding fact of this cross is the extent of dominance shown by the dwarf parent.

Raspberry.—Bailey (1898) believed that the purple raspberry, *Rubus neglectus*, was a natural hybrid between the black and red varieties. This was definitely proved at the Geneva Station by a cross between Smith No. 1, a black raspberry, and Lonhoro, a red seedling, which gave 209 purple raspberries (Wellington, 1913, Anthony and Hedrick, 1916). The same Smith No. 1 crossed with June, a red raspberry, gave 50 purples and 46 blacks. Selfed seedlings of Columbian, a purple variety, gave 31 purple, 7 red wine, 2 reddish, 1 yellow, and 1 black. The mode of inheritance of colors can not be determined, although it seems that several of the black varieties are heterozygous for color and that several

factors for color are present. The presence of bloom on the canes proved to be a partially dominant character over the absence of bloom. The number of spines on canes showed segregation in selfed seedlings of Columbian. Yellow raspberries could be told in the seedling stage from the black and purple by the absence of red tinge on the leaves. The production of promising varieties from crosses between the red and black varieties was especially mentioned.

The Van Fleet raspberry may be mentioned as an example of an improved variety that has been produced by hybridization (Darrow, 1924). A representative *Rubus innominatus* introduced from China was crossed with the Cuthbert red raspberry. The new form is productive, relatively disease resistant, and ripens berries over a period of four or five weeks, beginning at the time when the last red raspberries have been harvested. The less desirable characteristics of the new variety are its medium size and softness of fruit.

Strawberry.—The inheritance of flower color was found by Richardson (1918) to show the usual color dominance, pink over white and controlled by two factors. It was also found that singleness dominated over doubleness and was dependent for its expression on a single factor. Valteau (1923) obtained evidence in support of the chromosome theory of inheritance of sex in the strawberry. The data indicated that staminate and hermaphrodite plants were homozygous and pistillate plants heterozygous for the sex chromosome.

Grape.—The Geneva Experiment Station, in New York, (Hedrick and Anthony, 1915) likewise furnished the greater part of our data on inheritance of characters in the grape. Table XCVII gives the results of crosses for skin color.

TABLE XCVII.—INHERITANCE OF SKIN COLOR IN GRAPES

Color of parental types	Color of seedlings			
	Black	Purple to dark red	Medium to light red	White
White × white.....	166
Light red × light red.....	8	6	13	8
Dark red × dark red..	38	43	45	42
Black × black	407	49	13	54
White × dark red ..	5	44	14	50
White × black.....	41	3	3	12
Black × dark red...	100	52	40	32

The chief conclusions which may be reached from these results are that nearly all varieties are heterozygous for color and that white is a pure recessive.

In studies of inheritance of quality there is a proof of the value of selecting as parents the types which excel for the character being worked with. Table XCVIII gives some of the results of crosses in which quality was studied.

TABLE XCVIII.—INHERITANCE OF QUALITY IN THE GRAPE

Parental types	Total	Percentage of good or better
Parents good or of higher quality.....	682	27
Good × fair or poor.....	56	11
Medium × medium.....	213	10
Poor × poor.....	51	4

Nearly all grapes of high quality at the New York station contain some *V. vinifera* blood. This is easily understood when one remembers the long period of breeding of the European varieties and that American varieties were only recently obtained from the wild. Inheritance of size of grape berry and ripening period showed the value of selecting as parents varieties which excel in the character which the breeder wishes to obtain.

Peaches.—In crosses between nectarines and peaches, Becker (1923) obtained peach-like fruit and in crosses between nectarines, only nectarines were obtained, indicating that pubescent fruit was dominant to smooth. Resistance to nematode in the peach is apparently an inherited character as has been shown by McClintock (1923). Perhaps the most extensive inheritance studies in the peach are those reported by Connors (1923). In crosses between Greensboro (spreading) and Crawford (upright) the F_1 seedlings were intermediate in habit of growth and since spreading, open trees are preferable for orchard purposes, it is desirable to use as one parent either the spreading or intermediate type of tree. With respect to size of blossoms the large and small ones were found to be homozygous and the intermediates heterozygous. The latter segregated into one large, two intermediate, and one small blossom. A further study of the correlation between the color of the inside of the calyx cup and of the fruit flesh, first pointed out by Hedrick, was made. A green calyx cup is correlated with white flesh and an orange-colored calyx cup with yellow flesh. Moreover, a green, white, or pale cream calyx cup indicates a homozygous white flesh, a yellow-cream to yellow-buff calyx cup indicates a heterozygous white flesh, and a deep orange-colored calyx

cup indicates a yellow flesh. White flesh is dominant to yellow and its inheritance is apparently controlled by single factor difference. Several other characters were studied but their exact manner of inheritance was not determined. One of the most interesting results of this investigation was the determination of prospective parents which would be most likely to yield progeny of economic value. As a direct result of this work, the New Jersey Experiment Station is offering to the public several new varieties of peaches.

Illustrations of Methods of Breeding.—Methods of breeding fall naturally under three main heads;

1. Selection of bud sports.
2. Seedling selection.
3. Controlled crosses.

As has been already mentioned many of our varieties have resulted from chance seedlings, others from seedlings in which only one parent was known. A review of the subject leads to the conclusion that the improvement of fruits by the use of self-fertilized seed is a less desirable method than by the use of crossed seed. When selfed seed can be produced the progeny are as a rule less vigorous than those obtained from crossed seed. As these subjects have been touched upon in some detail under other headings, seedling selection will not be discussed further.

Selection of Bud Sports.—It is now a commonly accepted fact that mutations or sudden changes in the germinal material do occasionally occur. Likewise, in asexually propagated species bud sports have been found, and in some cases these have been used as the foundation of improved races. To justify a method of breeding founded upon their utilization, such bud sports must occur frequently enough to pay for the trouble of making a systematic search for them.

A review of the experimental evidence is of considerable interest, for this is the only means we have of deciding whether the selection of particular trees or branches for propagating purposes is a reliable means of producing new varieties. Of the four apple bud sports mentioned in Table XCII the chief changes were in the color of the fruits. In the Isabella grape several sports were obtained which produced black grapes of larger size than Isabella, and which excelled in sweetness (Powell, 1898, cited from Dorsey, 1916). Dorsey (1916) records two large-fruited variations in the Concord grape which arose as bud sports.

Instances of bud variations in ornamental horticultural plants are quite common. As an example of their frequency, the work of Stout (1915) will be briefly discussed. Extensive asexual or clonal selections were made in *Coleus* and numerous color changes were isolated as well as changes in leaf shape. The same variations were obtained through bud sports as by seed reproduction. Some clonal lines sported much less frequently than others.

The work on citrus fruits (Shamel and others, 1918) which has been carried on in California, has drawn the attention of many horticulturists and plant breeders to the subject of bud sports and their place in correct fruit-breeding methods. Valencia oranges were originally introduced from three sources, but all have proved of similar type and are now called Valencia. From this variety, 12 important strains originating as bud sports have been isolated. As a rule, single off-type branches produce fruits showing characters which are different from the fruits borne on the remainder of the tree. Many of these sports are of highly undesirable type. The Washington navel orange was introduced from Brazil in 1870 by the Department of Agriculture at Washington. Thirteen distinct strains have been isolated through bud selection. Thompson, one of these strains, has proved a very desirable type. Likewise, bud sports have occurred in the grapefruit which was introduced in California from Florida in 1890. The Marsh is the best of six strains which were obtained by selecting bud sports. Similarly, bud sports have occurred in lemon orchards. Shamel (1919) records an occurrence of a sporting branch in a French prune tree which was first observed in 1904. Several grafts from this branch were placed in bearing trees. These grafts reproduced the characters of the sporting branch. In 1914, trees in alternate rows of an orchard were top worked by the use of buds from the new strain and compared with buds from the normal French prune variety. The top-worked trees from the bud sport bore larger fruit than those from the normal prune. The fruits were also more evenly distributed over the tree than in the original French prune variety.

Those mentioned are some of the more striking instances of the production of new varieties through the isolation of bud sports. Crandall (1918) has made an extensive test in Illinois of the value of bud selection in apples as a means of improving the variety. Two distinct lines of study have been followed.

1. The value for propagating purposes of buds selected in different ways. The experiments included a comparison of large *versus* small buds, of buds from different parts of the tree and from different locations on the shoot.

2. Selection of trees because of special merit. Comparison of seedlings produced from large and small apples produced by these selected trees.

A considerable number of varieties was used for the first study and a total of 5,400 buds were selected. A careful measurement was then made of the yearly growth of wood from the buds which had been previously selected. Growth curves were made and, on the basis of these results, the conclusion was reached that all buds from healthy shoots were of equal value for propagation purposes.

The characters of seedlings grown from seeds of large and small fruits borne on trees of special merit were carefully studied. Seeds from large

fruits produced seedlings which were somewhat more resistant to adverse conditions than seedlings grown from small fruits. The hypothesis that this may be explained by the fact that large fruits and large seeds frequently occur from crosses, seems reasonable in the light of the work of Lewis and Vincent previously cited.

Stewart (1912) has discussed the value of cion selection in tree-fruit improvement. Individual apple tree data over a period of from ten to fourteen years were presented. Under apparently the same conditions some trees were consistently higher yielders than others. A review of considerable experimental evidence led Stewart to conclude that there was more evidence in favor of purity of the clone than in favor of the value of clonal selection as a means of producing higher-yielding strains. Similar conclusions were reached from an experiment carried on by Tyson Brothers, in New York, with the York Imperial apple. Two trees were selected which bore unusually similar fruits and these were used for propagation. More than 8,000 trees were planted in the new orchard. Examination of trees of this orchard when they came into bearing showed them to be not superior to the usual York Imperial apple (Dorsey, 1917).

The cited cases show the present status of the problem of selection of bud sports as a means of improvement of fruit crops. The studies with the citrus genus appear to justify the belief that degenerate or inferior bud sports are of frequent occurrence. This leads to a conclusion that only those limbs which produce normally healthy fruit should be used for propagation purposes. Even among the citrus fruits there is as yet no very conclusive proof that the selection of cions from high-yielding trees will accomplish more than to prevent possible "running out" of the variety. The evidence from apples would seem to justify the belief that bud sports are very infrequent. The breeder, then, can well afford to make careful observations with the hope of discovering bud sports. If apparently desirable sports are found, these may then be used for propagation.

In such crops as citrus fruits and with such plants as *Coleus*, bud sports are of frequent occurrence. There is, then, some evidence for the belief that sports occur more frequently in heterozygous than in homozygous material. As Stout (1915) obtained the same changes through asexual selection as by the use of self-fertilized seed, it seems reasonable to suppose that some sort of segregation and recombination occurs in somatic tissue. No cytological evidence has been given to account for such a supposition. With heterozygous material the loss of a single dominant factor would be immediately apparent in the soma. This is one reason why bud sports occur more frequently in heterozygous forms (East and Jones, 1919). Nabours (1919) has shown that similar cross-overs occur in parthenogenetic reproduction in the grouse locust as in those forms which are produced by the recombination of gametes containing the haploid number of chromosomes. If the usual sort of cross-

overs occurred in homozygous material, there would be no change in the homologous parts of chromosome pairs. In heterozygous material, however, new combinations of factors would be produced which might cause changes in the external appearance of the organism. No cytological basis for such cross-overs has been demonstrated.

Controlled Crosses.—One of the earliest controlled experiments in the breeding of fruits by crossing was started by Swingle, in 1893, in Florida. This was an attempt to produce hardier types by the use of wild citrus species. The hardy Chinese species, *Citrus trifoliata*, was used as one of the parents. In 1897, 212 crosses were made between this species and orange varieties. The three fruits that were produced gave thirteen hybrids, which were so different from existing varieties of citrous fruits that they were called "Citranges." Other crosses between citrous species were made. One of the promising combinations was a cross between the West India lime and the kumquat orange. This orange is one of the hardiest of the evergreen citrous trees while the lime is very tender. Further experiments are under way and other promising wild relatives of the citrous fruits have been obtained. Crosses of this nature are producing fruit varieties which are successful in regions where citrous fruits could not be grown formerly. The work shows the necessity of a thorough botanical knowledge of the wild relatives of the crop which it is hoped to improve by breeding.

A somewhat similar method of work with the hope of producing hardy apples for the Canadian Northwest was started by William Saunders in Canada in 1888. The wild Siberian crab, *Pyrus baccata*, which proved hardy on the prairies and withstood temperatures of 50° below zero, was used as the female parent and crossed with commercial apple varieties. Macoun (1915) states that the fruit of *Pyrus baccata* averages $\frac{1}{2}$ inch in diameter and is quite astringent. The fruits obtained from some of the more promising of the crosses were not so large as desired, although some compared very favorably in size with ordinary crabs. They were of good flavor and proved hardier than any varieties of apples and crabs that had been tested up to that time. Several are here listed.

Jewel,	<i>P. baccata</i> × Yellow Transparent.	Size 1.4 by 1.3 inches
Columbia,	<i>P. baccata</i> × Broad Green.	Size 1.8 by 1.6 inches
Charles,	<i>P. baccata</i> × Tetofsky.	Size 1.6 by 1.5 inches

Recrosses between the best of these and apple varieties were made and 407 trees were grown. Some varieties were obtained with larger fruits but these as yet have not been thoroughly tested for hardiness.

Pears have been frequently tried in the Dakotas but have failed for two causes (Hansen, 1915): (1) lack of hardiness; (2) susceptibility to blight. The Chinese sandpear, *Pyrus sinensis* Lindley, obtained from Dr. Sargent, of the Arnold Arboretum, proved perfectly hardy and

resistant to blight. Various crosses between this species and cultivated pears belonging to *Pyrus communis* have been made. Preliminary tests have shown that some of the seedlings were blight resistant and hardy. These results indicate that the problem of producing pears for the Northwest may eventually be solved. In a somewhat analogous manner, Hansen (1911) has produced new plum varieties by crossing the native

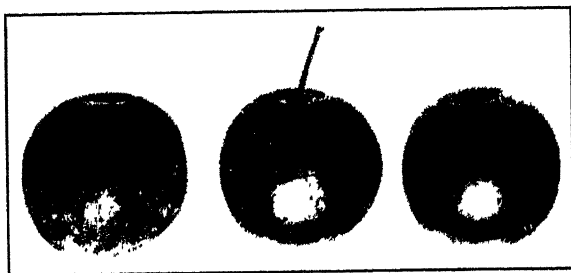


FIG. 69.—Wolf, a hardy variety of plums which lacks quality of fruit. (Photo loaned by Dorsey.)

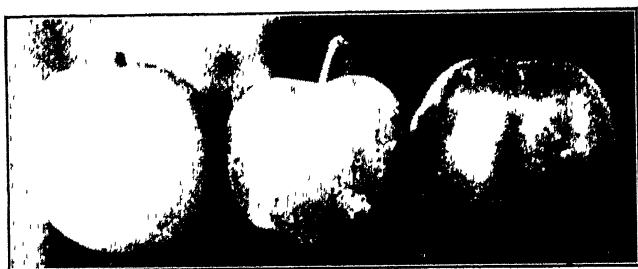


FIG. 70.—Burbank, a plum of high quality produced by Luther Burbank. It lacks hardiness when grown in Minnesota. (Photo loaned by Dorsey.)

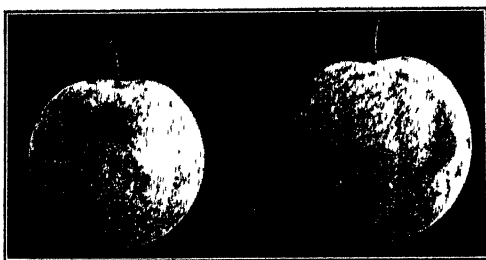


FIG. 71.—Tonka, Burbank \times Wolf, No. 21. Has high quality and is nearly as hardy as the hardy variety of Wolf. (Photo loaned by Dorsey.)

sand cherry with Japanese plums. This has resulted in a "happy combination of hardiness, rapid growth, and early bearing of tree, with large size and choice quality of fruit."

It will be of interest here to present briefly an instance from the fruit-breeding work at the Minnesota Station in which desirable new plum hybrids were obtained when the tender parent, Burbank (*P. triflora*) was

crossed with Wolf which is a hardy variety of *P. americana mollis*. The percentage of hybrids killed during winter dormancy is taken as a basis for classification. It will be seen that some of these hybrids, as No. 8 or No. 9, are hardy in the bud like the staminate parent Wolf. The two which have been named Red Wing and Tonka, are intermediate in hardiness but of excellent fruit characteristics.

TABLE XCIX.—SHOWING THE PERCENTAGE OF BUDS KILLED IN AN F_1 PROGENY WHEN ONE OF THE PARENTS IS HARDY AND THE OTHER TENDER¹

Parent	Percentage of buds killed, 1916-17	Parent	Percentage of buds killed, 1917-18
Burbank.....	100	Hybrid No. 9.....	0
Wolf.....	0	10.....	50
Hybrid No. 1.....	50	11.....	1
2.....	35	12 (Red Wing).....	10
3.....	5	14.....	25
4.....	5	15.....	5
5.....	10	16.....	5
6.....	10	17.....	0
7.....	0	20.....	25
8.....	0	21 (Tonka).....	25

¹ Data furnished by M. J. Dorsey.

These few instances have been given as indicative of the methods of work which are being used by some of the most progressive fruit breeders. Some general conclusions regarding methods of work may be here given.

1. A knowledge of the botanical relationship and wild relatives of the fruit are necessary if greatest progress in improvement is to be obtained.

2. Some varieties and species transmit their characters to a much greater degree than do other varieties. A knowledge of the more potent varieties materially aids in planning a cross.

3. Varieties selected as parents should contain in the highest degree possible the character or characters desired in the progeny.

4. The larger the numbers of progeny grown, the greater the chances of obtaining the combination desired.

5. Most fruit crosses give variable progeny in F_1 . Numerous crosses should, therefore, be made. When possible large F_2 generation progenies should be grown from the more promising F_1 types. Crosses of different F_1 types may give the desired combination in F_2 .

6. Information regarding the mode of inheritance of particular characters will assist in selection of varieties to be used as parents.

CHAPTER XXI

FARMERS' METHODS OF PRODUCING PURE SEEDS

The production of new varieties of farm crops is a specialized line of work and should be undertaken as a rule only by men who have had special training in crop breeding. The expense and time necessary for this kind of experimental work are too great for the individual farmer. The aim of the farmer or seed grower should be to maintain the improved form and not to allow contamination through crossing with inferior stock, admixture, plant diseases, etc. A method of producing seed which will stand this test and at the same time meet with the approval of the farmer must be simple, effective, and inexpensive. A nation or state cannot afford to maintain an experimental laboratory only to have the products of that laboratory deteriorate because of subsequent treatment. The maintenance of pure, improved varieties as well as their discovery by selection or synthesis by crossing is an essential factor in economic food production. Before taking up in detail methods of producing pedigreed seed by farmers, a few observations regarding seeds in general will be made.

DETERMINATION OF BETTER VARIETIES

Certain general facts regarding varieties should be understood. The breeder and grower must recognize that no one variety is best adapted to a particular locality or for all seasons. In some seasons an early oat gives the best yield. Owing to slight seasonal variations, a later variety may excel in yield. Thus, a single season's test is not reliable as a means of determining the better sort to grow. For this reason carefully conducted tests are carried on each crop season. By means of these, the experiment stations are in a position to determine and advise as to the better varieties. The final decision as to which variety to grow must of course be made by the farmers and based on their actual field experiences.

WHAT IS GOOD SEED?

There are certain characters of farm crops which must be considered if the grower wishes to produce good seed. Good seed of any farm crop must belong to a variety that is superior in the following respects:

1. Adaptability to the locality and soil.
2. Yielding ability.

3. Purity to type for small grains or self-pollinated crops, and comparative purity for corn and other cross-pollinated crops.
4. Quality for the particular characters for which the crop is grown.
5. Hardiness.
6. Erectness or ability to withstand lodging.
7. Disease escaping or resistance to disease.

The seed of the particular variety itself must be superior in the following:

1. Germinating ability.
2. Good color, plumpness and weight.
3. Uniformity.
4. Freedom from diseases transmitted by seed.
5. Freedom from any other damage.
6. Freedom from obnoxious weeds.
7. Freedom from mixture with other varieties.

Adaptability.—We have already indicated that no one variety always excels in yield or quality. All that the experiment stations can do is to determine the few better varieties and in this way assist the farmer to decide which to grow.

There are decided advantages in limiting the number of varieties. It is of considerable value for one locality to produce large quantities of a particular variety. Several reasons are apparent, chief of which are: (1) the buyer can obtain a large amount of seed of that particular variety; (2) the production of only a few varieties or a single variety is of material help in keeping purity of type, as there is not so much opportunity for (a) mixtures in thrashing, growing, etc., or (b) cross-fertilization between varieties, which causes variability of seed and plant characters and, therefore, loss of purity of type.

Yielding Ability and Quality.—Variety tests carried on under experimentally controlled conditions are the best means of determining comparative yield and, to some extent, comparative quality of different strains. Many farmers sustain annual losses, which are not small, due to using seed of an overexploited variety which has not proved its worth in competitive tests. With many crops, quality is of prime importance and must receive some consideration if a No. 1 grade product is to be obtained.

Purity.—For crops like wheat, oats, and barley, which are self-fertilized, uniformity is the rule, providing the grower is willing to pay some attention to eliminating accidental mixtures. For cross-fertilized crops, of which corn is a good example, purity of type is of less importance, although certain general standards of purity are desirable.

Hardiness.—Hardiness is a feature of adaptability but it deserves especial mention. Ability of annual crops, like rye and wheat, to withstand winter-killing as well as winter hardiness for perennial crops, such

as alfalfa, is of high importance and is generally given much consideration by experimenters before recommending a particular variety

Strength of Stalk.—Ability to stand up, which obviates injury from lodging, is of much importance in grain and hay crops. In small grains early lodging often causes shriveled seeds. The difficulty of harvesting is greatly increased when the crop is flat.

Seed of the Variety Chosen.—By using the above-mentioned characters as a guide, one may intelligently choose the variety which satisfies best the particular conditions. The next problem is to obtain high-grade seed of the variety and it is obvious that seed cannot be high grade unless it possesses vigorous germinating ability. Color, plumpness, and weight are all important in that they indicate maturity and whether or not the seed was damaged by heat or mould. If seed with a relatively high moisture content is improperly stored, it very often becomes discolored and mouldy. It is possible to obtain a more even stand with seed uniform in size. High-grade seed should be free from disease. The organisms which cause such diseases as the smuts of oats and wheat are carried on the surface or within the seed. Seed is sometimes damaged in threshing. This is true particularly of the large-seeded legumes. If soybeans or field peas are thoroughly dry and threshed with a high-speed cylinder a considerable amount of split seed usually results. Another important quality of desirable seed is its freedom from obnoxious weed seeds. Most farmers would be very hesitant about purchasing seed which contained seeds of quack grass, Canada thistle, wild onion, or dodder. Lastly, high-grade seed must be free from admixtures of other varieties. In the regions where spring wheat is grown a relatively small amount of Humpback wheat contained in a variety like Marquis lowers very materially the value of the latter for seed.

METHODS OF SEED PRODUCTION

After obtaining the better variety for the locality, the seed grower has the problem of keeping this variety in the same high state of production and if possible to improve it. The purpose of this chapter is to outline methods for the various crops which may be used by the seed grower or by the average farmer.

Among farm crops, the production of seed generally depends on a union of the male reproductive cell, contained in the pollen grain, with the female reproductive cell—the egg cell.

The pollen grains of corn are produced in the tassel and each thread of silk leads to an ovary which contains the egg cell. In order to produce seed, the male reproductive cell must pass down through the silk and unite with the female cell. This process is called fertilization. If pollen and silk are borne by the same plant the process is self-fertilization,

and if by different plants, cross-fertilization. As the egg cell and the pollen grain of self-fertilized plants are, as a rule, alike in their inherited characteristics, the progeny of a single self-fertilized plant, such as barley, wheat, or oats, have the same inheritance. There is, of course, considerable variation in all characters, owing to environmental effect, but all evidence shows that these differences are not truly inherited. Occasional crosses occur in self-fertilized crops which cause inheritable variability. Mass selection serves to eliminate these off types.

SEED GROWERS' METHODS FOR SELF-FERTILIZED PLANTS

For self-fertilized plants the grower can, as a rule, obtain a pedigree strain which is nearly adapted to his conditions. The only thing that he can do with this variety is to save seed in such a way that mixtures of other strains or occasional crosses are eliminated, together with obnoxious weed seeds and diseases. The strain in question can be kept in a pure condition for its characters, and if it is not entirely pure at the outset a correct method of seed selection will tend to purify it and thus to increase its value. The work for self-fertilized crops is very simple as compared with the production of improved seed of cross-fertilized crops or the production of highly bred livestock. For self-fertilized crops the method outlined below is essentially that which is compulsory for the production of registered seed by the Canadian Seed Growers' Association. Formerly the growers of registered seed were required to maintain a yearly hand-selected seed plot, but at present this is not required. Registered seed may be produced from Elite Stock seed or from other registered seed for an indefinite number of generations providing the crops meet the requirements of a rigid system of field inspection. The essential steps in the production of registered seed are:

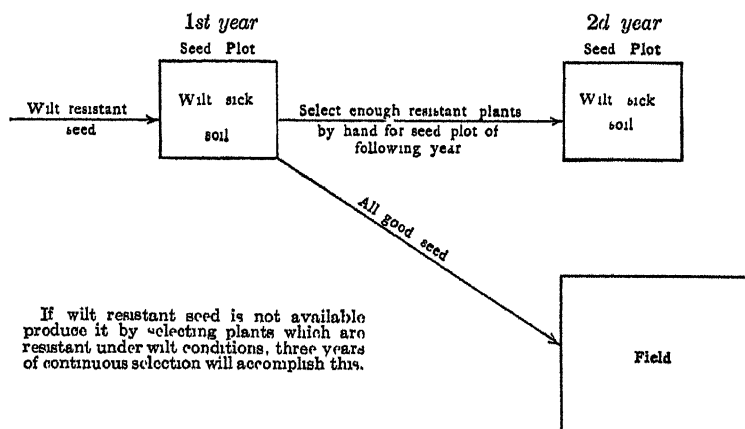
1. The seed of a variety must be obtained from a source approved by the Association.
2. The crop must be grown on land on which the previous crop did not consist of a similar crop except it be of Registered or of Elite Stock seed of the same variety.
3. The area on which the registered seed is produced should be separated from other similar crops by a distinct space.
4. The crop should be free from weeds the seeds of which cannot be thoroughly removed by machinery.
5. A very high percentage (99.99 per cent) of purity must be maintained with respect to variety and also with respect to other kinds of crops except those which can be thoroughly removed by machinery.
6. The crop should be reasonably free from diseases.

For the tobacco crop there is no necessity of a seed plot. The grower should select good-type plants in the field and save these for seed pro-

duction. The best growers insure the production of self-fertilized seed by covering the inflorescence before any of the flowers open, with a 12-pound manila paper bag. It is necessary to remove the bag from time to time to shake out the dead parts of the corolla so that the seed will not become damaged. Ten or twelve plants handled in this manner furnish sufficient seed for a large acreage.

If the farmer is troubled with flax wilt he can easily overcome this difficulty by seed selection. All that is necessary is to select from a plot on which the wilt disease is causing considerable loss those plants which appear to be free from the disease. Experiments carried on by Bolley at the North Dakota station, which have been corroborated at Minnesota (Stakman, *et al.*, 1919), have shown that wilt resistant varieties can be obtained by selecting plants which appear resistant on wilt-sick soil. Barker (1923) has obtained evidence which proves that wilt-resistant varieties, when grown on wilt-free soil, retained their inherited quality for resistance for a period of three years. The same wilt-resistant varieties were grown continuously for a period of three years on wilt-free and wilt-infested soil respectively. A comparison of the relative resistance of the varieties grown under the two conditions showed no appreciable difference. For flax, the seed plot may be located on wilt-sick soil.

DIAGRAM OF METHOD OF CONTROLLING FLAX WILT BY SELECTION



For the farmer who does not care to use a seed plot according to a method somewhat as outlined for naturally self-fertilized crops, some progress may be made by taking certain precautions. When changing from one variety to another in threshing, it is well to operate the thresher empty for several minutes before beginning on the second variety. Then, too, it is well to discard the first few bushels threshed of the second variety. The grain which is to be used for seed should be carefully stored under conditions which will insure freedom from injury owing to rodents,

insects, or heat. The seed should be put through a fanning mill to remove weed seed, foreign matter, and light chaffy grains. Carefully conducted field experiments with wheat and oats have failed to demonstrate any superiority in yielding ability of heavy- over medium-weight seed. The fanning mill, however, is a valuable implement for removing impurities, cracked grain, and grains that are light in weight due to disease or immaturity. Grains of wheat which are light and chaffy due to wheat scab may be largely removed by means of an effective wind blast. If the seed is known to carry a plant disease which may be controlled by seed treatment, such treatment should be given.

IMPROVED CORN SEED

The determination of the better variety of corn to grow is not difficult. The farmer can obtain reliable advice from the local county agent or by consulting the nearest experiment station. The introduction of new varieties of corn from other states before they have been tested for the climatic conditions in question is a very undesirable practice and as a rule a cause of much annual loss to the corn grower. The problem with corn is somewhat different from that with the self-fertilized crops. Corn is cross-fertilized, therefore constant inherited variability is the rule. When a variety is introduced from another locality it undergoes a process of selection which may markedly change its characters. Selection in a pedigreed line of wheat, on the contrary, does not change its characters and serves only to keep the variety in the same state of purity by artificially removing any possible mixtures which may occur. This brief discussion will probably serve to show that seed selection on the farm is a very important practice for the corn grower, unless there is a local grower of high-grade seed.

The corn-seed grower faces another difficulty which the small-grain seed producer does not have to consider. With small grains--barley, oats, and wheat--purity for all characters is the general rule. This has led the corn breeder also to attempt to obtain purity of type. Carefully controlled investigations have served to show a possible fallacy in this practice. The report of a study at the Minnesota Station (Olson, Bull, and Hayes, 1918), which contains experimental evidence together with a review of other experiments in relation to score-card characters and yield, show no correlations between individual characters such as trueness to the ideal score-card ear type and subsequent yield of these ears.

Artificial self-fertilization in corn isolates homozygous types which are less vigorous than normally cross-pollinated plants. All other evidence seems to show that too close a purity of type in corn tends to a reduction in vigor. The grower whose method of selection is based upon ear type is certainly obtaining no gain in yield of shelled corn per acre. The detrimental results of too close selection to type may not be very apparent and

may be more than counterbalanced by the extra attention from a cultural standpoint, for an interest in ideal ear types certainly stimulates the farmer to produce better corn. It is not, however an increase due to better breeding but to better cultural practice.

The present purpose is to outline methods of seed selection. As there is little apparent relation between score-card characters for type of ear planted (within a particular variety) and resultant yield, even though such selection may be constantly practiced, little attention is paid to those characters as far as the breeding plan goes. The grower should, of course, produce corn of one variety which is pure, judged by easily evident characters, such as color of seed and cob. Abnormalities, such as very large butts, badly flattened cobs, or very irregularly rowed ears, should not be used as foundation stock. Aside from these there is no need of paying much attention to type. Ability of a variety to mature under the conditions, is very important and needs much attention.

In a bulletin of the Minnesota Station, Hayes and Alexander (1924) report the results of an experiment with different methods of corn breeding for the practical farmer. As a result of this work which was carried on with Rustler White Dent, the authors conclude that there seems to be little or no value from the farmer's standpoint of using the ear-to-row method of corn breeding and that certainly its continuous use appears undesirable. Close selection for ear type which is required by the ordinary score card brought about a small but significant reduction in yield. The experiment seems to indicate that selection should be on the basis of vigor and yield of the plants rather than on the basis of ear type.

In a study of data from four varieties of corn grown in ear-to-row plots, Richey and Willier (1925) found a positive correlation between weight of ear and yield and a negative relation between number of rows per unit of circumference of ear and yield and also between number of kernels per unit of length of ear and yield. Positive correlations less marked and not so consistent were found between yield and length of ear, weight of cob, and circumference of butt of ear. It is concluded from this study that the selection of longer, heavier ears with proportionately heavy cobs and with relatively few rows of wide, thick seeds is justified, but that further selection on the basis of ear characteristics is futile from the standpoint of obtaining higher yielding corn. Smith and Brunson (1925) have obtained similar results.

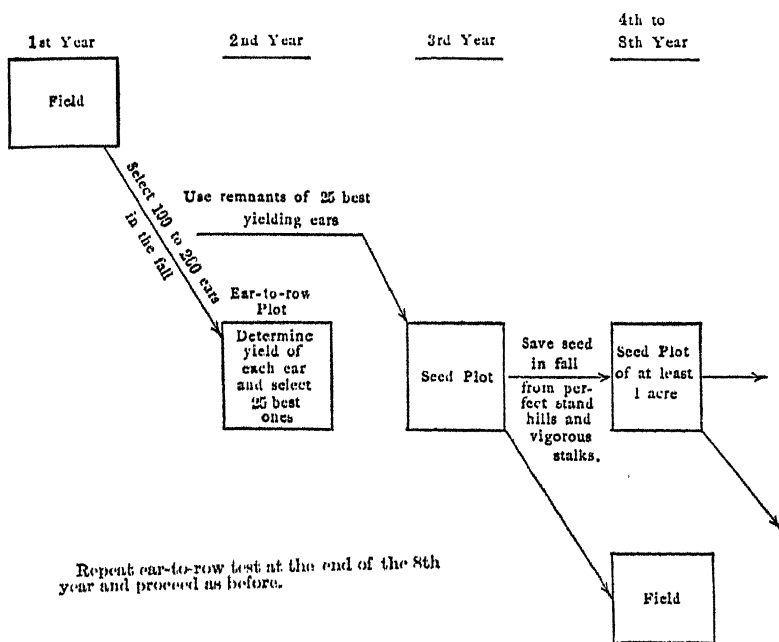
In a bulletin of the Illinois Experiment Station, Holbert, *et al.* (1924), have pointed out the marked reduction in yield that is caused by the root-, stalk-, and ear-rot diseases of corn. It is estimated that where infected seed is used the loss from diseases including smut and rust may conservatively be placed at 20 per cent. The writers found that the disease-free condition was more frequently associated with corneous, slightly indented seed than it was with starchy, deeply indented seed.

The most practical methods for the farmer to use in combating diseases of corn are crop rotation, selection of ears in the field from apparently disease-free plants and testing the ears for the presence of disease.

AN EAR-TO-ROW METHOD OF CORN BREEDING

Until recently nearly all discussions of corn breeding were based on the ear-to-row method. Such a method takes considerable time and can be carried out only by the breeder or occasional seed specialist. In adapting corn to new regions, the ear-to-row method may be somewhat more rapid than mass selection. The ear-to-row test consists of growing the seed of a certain number of ears in individual rows and determining the better yielding ones. Each ear saved is then a basis of further selection. Com

DIAGRAM OF PROCEDURE FOR SPECIAL CORN BREEDER



plicated methods have been used for the introduction of new blood and to keep up the vigor of the strain. The method here outlined is an attempt to simplify this practice and at the same time obtain as good results as can be obtained by the more detailed procedures. It is based on experimental studies carried on at the Nebraska Station (Montgomery, 1909). The details are as follows:

1. Select from 100 to 200 ears of the variety to be grown. If possible, select these ears in the field from those apparently disease-free stalks which, if in a perfect stand, will give a good yield.

2. Make an ear-to-row test of these selected ears, saving half of the seed from each ear planted. From this ear-to-row test the 25 best ears may be determined.

3. Mix the remnants of the 25 highest yielding ears and plant the following year in a seed plot. Select all ears obtained which are fairly desirable, eliminating only the very undesirable types.

4. Use the selected seed for planting as much of the corn acreage as possible.

5. Give special attention to a part of the field so that a uniform stand may be obtained. Select enough seed from this part of the field for the entire acreage. Select seed for the following year's seed plot in the fall before a killing frost, from perfect stand hills and from those stalks which appear free from disease and which under competition show ability to produce one or more good ears. Throw away only the ears of very undesirable type.

6. Continue the method outlined under 5 for a period of four or five years and then use again the ear-to-row method as outlined under 1 and 2.

METHOD OF CORN BREEDING FOR AVERAGE FARMER

The method here outlined is very simple, yet it is probably as effective as the more complicated ear-to-row method in maintaining or increasing production. In the plan suggested below a special seed plot may or may not be included. However, it is well to select seed ears from a field planted by the hill method and in which there is as nearly a perfect stand as possible. Vigorous ears borne on plants growing in close competition probably are vigorous because of their inheritance. The following steps are suggested for this method of corn breeding:

1. Choose a variety that is adapted to the particular location. It is safer to obtain seed from a high-yielding corn in the neighborhood than from a distant locality.

2. Select mature ears in the field before a killing frost from vigorous stalks growing in competition with other stalks. Select ears from three or four stalk hills surrounded by other three or four stalk hills. Select ears borne at a convenient height with their tips covered with husk.

3. Never select ears from stalks which show symptoms of disease. Some of the indications of disease are: smut balls, broken shanks, a shredded or discolored scar where the ear was broken from the shank, a broken or lodged stalk, a weak growth, and premature ripening. The leaves and stalks should be quite green even after the husk on the ear is partly dry.

4. Select at least twice as many ears as will be needed for seed. Discard only the very undesirable ears.

5. Dry all the ears in a well-ventilated room. It is important to have each stored in such a way as to allow a free circulation of air around it.

6. Late in winter or early spring test for germination. In localities where it has been shown to be desirable, test each ear for germination and the presence of disease.

POTATO SEED (TUBERS) SELECTION

One of the most important factors in the production of high-quality potato tubers for planting is the control of potato diseases. Investigations carried on during recent years have shown conclusively that such diseases as mosaic, curly dwarf, leafroll, blackleg, and wilt, which may be transmitted vegetatively to the next generation, may bring about a marked reduction in vigor of the potato plant and a lowering of its yielding capacity. Much of the so-called "running out" in potatoes is caused by diseases.

From the foregoing observations, it is clear that every precaution should be exercised, first, to obtain disease-free seed stock and, second, to grow the plants under conditions which will reduce the risk of disease infection to a minimum. The latter perhaps may be realized best by growing the potatoes which are to be used for seed in an isolated field or plot which is at least 100 yards from any other field of potatoes since insects, such as aphids, may convey certain diseases like mosaic. Seed potatoes should be grown on a field that has not grown potatoes for several years, and certainly on one that was not in potatoes the preceding year. It is also important to give the necessary attention to seed treatment and spraying, if one wishes to combat successfully the various plant diseases.

In addition to the elimination of diseases, it is, of course, important to grow a standard variety with a high market demand and one that is free from admixtures with other varieties. Ordinarily the plants grown from tubers of a single plant are alike except for the occasional changes which occur in the inherited characters of the plant itself. Mixture in commercial tubers is one common cause of lack of purity of type. The selection of tubers, therefore, gives the grower an opportunity to improve his variety. It is important that the hills selected by hand be from a field relatively free from disease and of the best obtainable variety. In both methods suggested, it is highly desirable to maintain isolated seed plots.

With the foregoing general consideration in mind one may work out a method best suited to the particular conditions for producing seed tubers of high quality. The grower may obtain his seed stock from a reliable source, such as the producer of registered or certified seed, or he may produce his own seed stock. In the latter case he may proceed somewhat as outlined below.

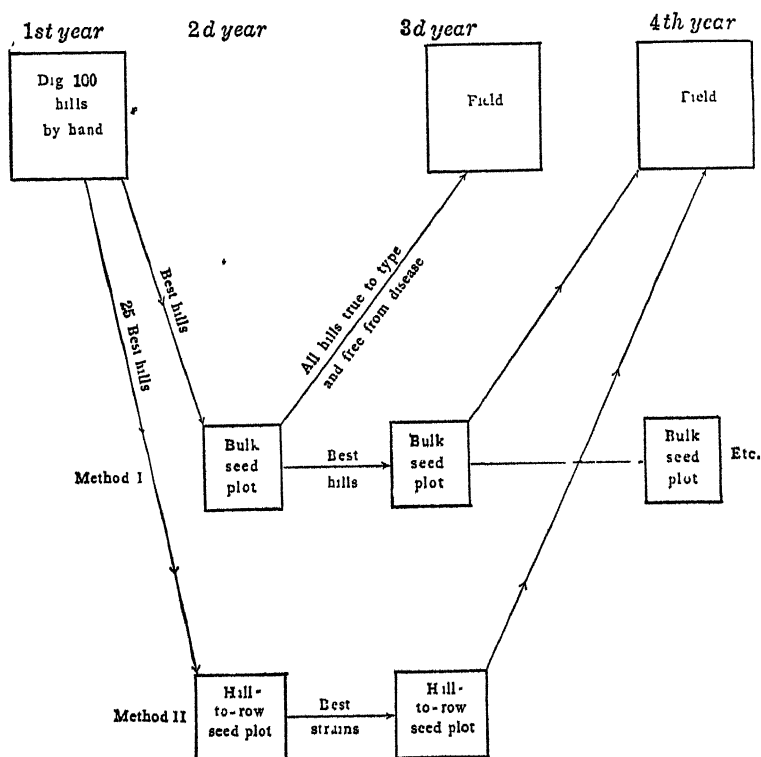
First Year.—(a) Remove from the part of the field used for saving tubers all plants which show evidences of diseases. This should be done during the growing season.

(b) At harvest time dig at least 100 hills by hand, keeping each hill separate.

(c) Use tubers from a number of the better hills for the stock plot the following year.

Second Year. Method I.—Plant all good tubers from previous year's selection of best hills in an isolated bulk seed plot. Enough tubers should be used to plant about $\frac{1}{4}$ acre. This requires approximately 5 bushels, which allows some tubers to be discarded.

DIAGRAMMATICAL ILLUSTRATION OF TUBER SEED PLOT SELECTION OF THE POTATO



Method II.—This is the hill-to-row method. In order to compare the productive capacity of each selected hill, it is desirable to have each row the same length and planted from the same total weight of potatoes. All of the progeny of some hills will be discarded this second year. Those that give a good yield and are desirable in other ways may be further tested.

Third Year. Method I.—Continue the stock plot by the same means as used in Method I for the second year's work, and use all good tubers produced each year in this seed plot for field planting. This work may be continued each succeeding season by the same plan.

Method II.—Make a further test of the best selections as determined by the second year's test, growing much longer rows, thus obtaining more reliable results. All tubers free from disease, of the best yielding strain or strains, may be used to increase the stock the following year.

The essential features of these two methods are presented on page 378 in diagrammatical form. Method II probably is somewhat better if all details of the test are carefully performed. For the average farmer, Method I is less cumbersome and if constantly practiced would probably give about as good a result as Method II.

IMPROVEMENT BY SELECTION OF SUCH CROPS AS ALFALFA, CLOVER, AND GRASSES

Obtain, if possible, a variety which is especially adapted to the conditions. Breeding work should aim at producing a variety which excels in resistance to winter injury and to plant diseases and is also a high producer of hay and seed.

1. Obtain 3 or 4 pounds of the best available seed.
2. Plant in a seed plot isolated as far as possible from other crops of a like kind. Plant seed in rows 3 feet apart and plant two or three seeds in each hill, spacing the hills 2 feet apart in the row.
3. Remove all but a single plant from each hill when the plants are well started.
4. Keep the plot free from weeds.
5. Discard all weak plants from time to time as they become apparent.
6. Save seed of all desirable plants and increase.

The improvement of the class of crops here mentioned is somewhat more difficult than with small grains, corn, and potatoes, and should be undertaken only by the few seed producers who are willing to take the necessary trouble to carry out carefully the details as outlined. Controlled experiments at some of the state experiment stations and in Europe have shown that much gain can be obtained by such selection.

SEED REGISTRY OR CERTIFICATION

The production of superior seed by the farmer has been encouraged by many agricultural organizations, the most important of which are the crop improvement associations. Such associations were first formed in northern Europe, later in Canada, and in the United States. At the present time most of the states north of the Ohio and Missouri rivers and between the Rocky and Allegheny mountain ranges have organized state crop improvement associations.

These associations are made up of farmers who have organized for the purpose of producing improved seed. The work in any state is usually carried out in close cooperation with officials of the agricultural college in that state. In fact, the secretary of the association, who is usually the executive officer that looks after the inspection and certifica-

tion of seed, is often a member of the college staff. In some states, the inspection and certification of seed is in charge of the state department of agriculture but here again the work is usually carried on in close cooperation with the college of agriculture.

Seed which meets certain standards set up by the crop improvement associations is variously designated as pedigreed, elite, registered, certified, and approved. Unfortunately, all associations neither maintain the same standards nor designate seed of similar quality by the same name. In general, however, pedigreed or elite seed refers to stock which may be traced directly to its ancestor or ancestors. The experiment stations are the usual source of this seed and they, together with a few growers, increase it according to certain rules. Pedigreed and elite usually designate the purest seed obtainable.

Registered is frequently used to indicate seed that is not more than three generations removed from a hand-selected seed plot. The source of seed for this plot is frequently pedigreed or elite stock. Sometimes registered seed is separated into first, second, and third generation seed depending on the number of generations it is removed from the hand-selected plot.

In some states certified seed is used to designate seed of a quality similar to that indicated for registered seed in the preceding paragraph. In most cases, however, certified seed does not indicate as high a standard of purity as registered seed. Certified seed is high in quality but usually its ancestry is less definitely known and it does not trace directly back to a hand-selected seed plot. Approved seed, as defined by some seed associations, is similar to the certified seed but in some cases the term is used to designate seed of a somewhat lower quality and purity.

Seed Inspection.—Before the stamp of approval is placed upon a given lot of seed by the agent of a crop improvement association or the organization which handles seed registry and certification, it is usually necessary that it be grown according to certain rules and that it pass at least one field inspection and one bin or crib inspection. In the case of potatoes there are commonly two field inspections required. The field inspection is always made by a personal visit and in many cases the bin inspection is made in the same way. A representative sample of the seed is very often sent in to the inspector for final analysis and for future reference. To help defray the expenses of inspection, certification, etc., a small fee is charged to each grower applying for this service.

The Minnesota Plan for Certain Crops.—As examples of plans for seed registry and certification, the methods followed in Minnesota for certain crops and in Maine for potatoes are outlined below. The writers do not wish to give the impression that these plans are more desirable than others used elsewhere, but they are simply chosen as representatives of methods now in use.

In Minnesota the certification of seeds is in charge of the Minnesota Crop Improvement Association. There are three classes of improved seed, (1) Pedigreed (Elite), (2) Registered, and (3) Certified.

Pedigreed (Elite) seed is seed stock which has descended from an individual plant or group of plants, of which a definite performance record has been kept and which has shown itself worthy of distribution. The Experiment Stations and a few special growers use this seed as their foundation stock.

Registered seed is improved seed which has passed both a field and bin inspection and traces directly back to a special seed plot. Small grains as wheat, oats, etc., must be within three generations of such a seed plot, while corn must be selected from a special plot each year. The Experiment Station and a few special growers grow a certain amount of registered, first-generation seed every year. Growers throughout the state have considerable registered seed of second and third generation for sale.

Certified seed is high-grade seed which has passed a field-and-bin inspection but does not qualify as registered because it has not directly descended from a seed plot.

Inspection Requirements.—To qualify as registered or certified seed the stock must meet the adopted inspection requirements and comply with the state seed law.

A. For wheat, oats, barley, rye, flax, and other small grains the requirements are:

- a. 95 per cent or more pure as it grows in the field.
- b. Must be free from seeds of quack grass, cheat, Canada thistle, sow thistle, wild pea, mustard, and contain less than one¹ seed per pound of other weed seeds when prepared for sale.
- c. Not more than a trace of chaff, dirt, broken kernels, etc.
- d. Not more than a trace of weathered, scabby, or otherwise diseased kernels.
- e. Must be dry, plump, bright, of good color, and weigh within 1 pound of the official standard weight per bushel.
- f. Must germinate 90 per cent or more at the time of sale or according to the standard of vitality as recognized for good seed of the kind.
- g. Must contain not more than a trace of mixtures of other seeds; for instance, wheat may contain an occasional oat or barley kernel.
- h. Must be uniform in size and up to the commonly accepted standards for the kind.
- i. In the case of rye it must have been grown at least 20 rods from any other rye field.
- j. Field inspection must be made during the last three weeks previous to harvest.

B. For Corn:

- a. Must be grown at least 30 rods from any other variety or otherwise isolated to obviate cross-pollination.
- b. Must give evidence of 99 per cent or more purity.
- c. Must be dry, mature, well cured, germinate 90 per cent or more, and conform to the standard as recognized for good seed.
- d. The ears must conform to the standard size, type, color, etc., of the variety.

¹ This may vary with the season.

- e. The seed, when shelled for delivery, must be uniform and conform in size and shape of kernel to the variety ideal and contain not more than a trace of butt or tip kernels
- f. Field inspection must be made during the last three weeks previous to harvest.
- C. For Soybeans, Field Peas, Beans, and Vetch
 - a. Must give evidence of at least 90 per cent purity when growing
 - b. Must be 99 per cent or more pure when prepared for sale.
 - c. Must be practically free from disease in both field and bin
 - d. Must contain less than one-half of one per cent of broken seeds and not more than a trace of foreign material.
 - e. Must be typical of variety both growing and in bin
 - f. Must be of good color, mature, uniform, well cured, and germinate 90 per cent or more.
 - g. Must be subject to and inspected within three weeks of harvest
- D. For Clover, Alfalfa, Timothy, Bromus, and other Hay-crop Seeds
 - a. Must be 95 per cent or more pure according to the variety
 - b. Must be inspected in the field while in bloom
 - c. Must be bright, good color, dry, and germinate not less than 90 per cent including hard seeds.
 - d. Must contain not more than 2 per cent of brown seeds or foreign matter, nor more than a trace of other hay-crop seeds.
 - e. Must be free from dodder, quack grass, and Canada or sow thistle
 - f. In case of alfalfa, the seed source must be established by affidavit. Particular emphasis will be placed on purity of variety when given field inspection.
 - g. In case of bromus, it must be grown on a field free from quack grass.

If the particular crop passes the several inspections to which it is subjected and if it meets all the other requirements the seed is registered or certified as the case may be. The proper tags are issued to the grower and he is then at liberty to sell his seed under the brand given it by the Minnesota Crop Improvement Association.

The Maine Plan for Potatoes.—The certification of seed potatoes in Maine is in the hands of the State Department of Agriculture. There are three inspections required; two of the plants and one of the tubers. The first is made at the time the plants are in bloom, the second at a later date, and the third is an inspection of the tubers at shipping time. Additional inspections may be made at the option of the chief inspector.

Pre-requisites to Entering Potatoes for Certification.—It is recommended that potatoes entered for certification be grown upon land that was not in potatoes the previous season and which is isolated, as far as possible, from fields planted with other strains.

It is recommended that the seed be from certified stock, the field records of which have been secured from the inspection service. It is also recommended that the seed be as free as possible from common scab and rhizoctonia and be disinfected with corrosive sublimate.

It is required that the crop be well cared for and be kept reasonably free from weeds and from insect injuries. It is also required that Bordeaux mixture spray be used to control late blight.

All applications for inspection must be mailed to the State Department of Agriculture not later than June 15.

First Inspection in Field.—1. More than 1.5 per cent varietal mixtures will disqualify.

2. More than 3 per cent mosaic will disqualify; more than 2 per cent leaf-roll will disqualify; more than 2 per cent blackleg will disqualify; more than 2 per cent wilt will disqualify; more than 3 per cent other weak hills will disqualify. A combination of diseased and weak hills equaling 8 per cent will disqualify.

3. All weak and diseased hills, of the types mentioned, must be removed at once under the inspector's direction and supervision.

4. The inspector will disqualify if fields entered for inspection are nearer than 250 feet to other potatoes carrying more than a passing allowance for mosaic and leaf-roll.

Second Inspection in Field.—1. More than 0.5 per cent varietal mixtures will disqualify.

2. More than 2 per cent mosaic will disqualify; more than 1 per cent leaf-roll will disqualify; more than 1 per cent blackleg will disqualify; more than 1 per cent wilt will disqualify; more than 5 per cent spindle tuber will disqualify; more than 1 per cent weak hills will disqualify. A combination of diseased and weak hills equaling 7 per cent will disqualify.

3. All weak and badly diseased hills to be removed during inspection.

4. At this inspection, a sufficient number of hills per acre shall be dug in such a manner as to secure a representative sample. Five per cent producing conspicuously less than average yield or off types, such as spindle tuber or giant hill will disqualify. (In case of doubt, check results.)

Third Inspection at Shipping Time.—1. Maine certified seed potatoes shall equal or exceed United States Grade No. 1.

2. The inspector present at this inspection will be instructed to put up such seed stock as he would like to receive if he were the buyer.

3. Special care must be taken to remove all tubers of a long, spindling type.

SEED SERVICE ORGANIZATIONS

Crop improvement associations usually function primarily as agencies for certifying seed and for printing and distributing a list of the growers of improved seed but, other than this, they do not participate in any commercial activity. In a few states farmers have organized for the purpose of buying and selling adapted seeds of high quality. Where such a seed service company exists it usually functions as a selling agency of the Crop Improvement Association. A warehouse is usually maintained where suitable cleaning machinery is available for the various kinds of seeds. Perhaps the greatest service that such organizations render is that they offer a reliable source for obtaining adapted seed, particularly of red clover and alfalfa.

DEFINITIONS¹

Acquired Character.—A modification of bodily structure, function, or habit which is impressed on the organism in the course of individual life

Aleurone.—The outermost layer of the endosperm in cereals when it is rich in gluten.

Allelomorph.—One of a pair of contrasted characters which are alternative to each other in Mendelian inheritance. Often used, but with doubtful propriety, as a synonym for gene, factor, or determiner

Allelomorphism.—A relation between two characters, such that the determiners of both do not enter the same gamete but are separated into sister gametes.

Alternative Inheritance.—A distribution of contrasting parental or ancestral characters among offspring or descendants, such that the individuals exhibit one or other of the characters in question, combinations or blends of these characters being absent or exceptional

Anthesis.—The period or act of flowering.

Awn.—A bristle-shaped elongated appendage or extension, to a glume, akene, anther, etc.

Barbed.—Furnished with rigid points or short bristles, usually reflexed.

Biotype.—A group of individuals all of which have the same genotype.

Bran.—The coat of the caryopsis, consisting of pericarp and seed-coat united.

Caryopsis.—A one-seeded dry fruit with the thin pericarp adherent to the seed, as in most grasses.

Centgener.—Originally used by W. M. Hays, at the Minnesota Station, to refer to a 100-plant plot in which each seed was planted a certain distance from each other seed.

Chaff.—The floral parts of cereals, generally separated from the grain in thrashing or winnowing.

Chimera.—An association of tissues of different parental origin and genetic constitution in the same part of a plant.

Chromosome Hypothesis.—The hypothesis advanced by Morgan in which factors are arranged in the chromosomes.

Class.—In genetics a group that includes variates of similar magnitude.

Clone.—A group of individuals produced from a single original individual by some process of asexual reproduction, such as division, budding, slipping, grafting, parthenogenesis (when unaccompanied by a reduction of the chromosomes), etc

Coefficient of Variability.—A relative index of variation obtained by expressing the standard deviation in percentage of the mean.

Coupling.—Such a relation between two dominant genes that they have a more or less marked tendency to be included in the same gamete when the individual is heterozygous for both of the genes in question.

Cross.—Synonymous with hybrid.

Cross-fertilization.—The union of the egg cell of an individual with the sperm cell of a different individual, whether the organisms belong to the same or different genotypes.

¹ Many of the genetic definitions are taken from Shull (1915), Babcock and Clausen (1918), or others. Ball and Piper's (1916) papers on terminology have been used for agronomical terms.

Cross-over.—A separation into different gametes, of determiners that are usually coupled, and the association of determiners in the same gamete which are generally in different gametes.

Detassel.—To remove the tassel, as in maize.

Cryptomere.—A factor or gene whose presence can not be inferred from an inspection of the individual, but whose existence can be demonstrated by means of suitable crosses.

Determiner.—Synonymous with gene or with factor as applied in genetics.

Dominance.—In Mendelian hybrids the capacity of a character which is derived from only one of the two generating gametes to develop to an extent nearly or quite equal to that exhibited by an individual which has derived the same character from both of the generating gametes. In the absence of dominance, the given character of the hybrid usually presents a "blend" or intermediate condition between the two parents, but may present new features not found in either parent.

Dominant.—(1) A character which exhibits dominance, *i.e.*, that one of two contrasted parental characters which appears in the individuals of the first hybrid generation to the exclusion of the alternative "recessive" character. (2) An individual possessing a dominant character in contrast to those individuals which lack that character which are called "recessives."

Ear.—A large, dense, or heavy spike or spike-like inflorescence as the ear of maize. Popularly applied also to the spike-like panicle of such grasses as wheat, barley, timothy, and rye.

Emasculation.—The act of removing the anthers from a flower.

Endosperm.—The substance which surrounds the embryo in many seeds, as the starchy part of a kernel of wheat or corn.

Factor.—An independently inheritable element of the genotype whose presence makes possible a specific reaction or the development of a particular character of the organism which possesses that genotype; a gene or determiner.

Floret.—A small flower, especially one of an inflorescence, as in grasses and Compositae.

F₁, F₂, F₃, Etc.—First, second, and third, etc. generations following a cross.

Gamete.—A reproductive cell containing x number of chromosomes.

Gene.—Synonymous with determiner or factor.

Genotype.—The fundamental hereditary constitution or sum of all the genes of an organism.

Glabrous.—Smooth, especially without hairs.

Glume.—One of the two empty chaffy bracts at the base of each spikelet in grasses.

Grain.—Cereal seeds in bulk.

Group.—In genetics, a broad, general term for a complex of other categories and not for a complex of any particular category.

Head.—A dense, short cluster of sessile or nearly sessile flowers on a very short axis or receptacle, as in red clover or sunflower.

Heredity.—The distribution of genotypic elements of ancestors among the descendants; the resemblance of an organism to its parents and other ancestors with respect to genotypic constitution.

Heterozygosity.—The condition of an organism due to the fact that it is a heterozygote; the state of being heterozygous; the extent to which an individual is heterozygous.

Heterozygote.—A zygotic individual in which any given genetic factor has been derived from only one of the two generating gametes. Both eggs and sperms produced by such an individual are typically of two kinds, half of them containing the gene in question, the rest lacking this gene; consequently the offspring of heterozygotes

usually consist of a diversity of individuals, some of which possess the corresponding character while others lack it.

Heterozygous.—The state or condition found in a heterozygote.

Heterosis.—The increased growth stimulus often exhibited in the F_1 generation of a cross

Homozygous.—The state of being homozygous; the extent to which an individual is homozygous

Homozygote.—An individual in which any given genetic factor is doubly present, due usually to the fact that the two gametes which gave rise to this individual were alike with respect to the determiner in question. Such an individual, having been formed by the union of like gametes, in turn generally produces gametes of only one kind with respect to the given character, thus giving rise to offspring which are, in this regard, like the parents, in other words, homozygotes usually "breed true." A "positive" homozygote with respect to any character contains a pair of determiners for that character, while a "negative" homozygote lacks this pair of determiners.

Homozygous.—The state or condition found in a homozygote.

Hybrids.—The progeny of a cross-fertilization of parents belonging to different genotypes

Hull.—A term applied to include the lemma and palea when they remain attached to the caryopsis after thrashing

Hypostasis.—That relation of a gene in which its usual reaction fails to appear because of the masking or inhibitory effect of another gene; contrasted with "epistasis."

Inflorescence.—The flowering part of a plant

Keel.—A central ridge resembling the keel of a boat, as in the glumes of some grasses, etc.; also the inferior petal in the legume flowers

Kernel.—Matured body of an ovule, seed minus its coats

Lethal.—A genetic condition causing death.

Linkage.—The type of inheritance in which the factors tend to remain together in the general process of segregation.

Lodicule.—A minute scale at the base of the ovary opposite the palea in grasses, usually two in number, and probably representing the reduced perianth.

Mean.—The arithmetical average.

Mode.—The class of greatest frequency

Mendelize.—To follow Mendel's law of inheritance.

Multiple Allelomorphs.—Three or more characters which are so related that they are mutually allelomorphic in inheritance.

Mutant.—An individual possessing a genotypic character differing from that of its parent or those of its parents, and not derived from them by a normal process of segregation.

Mutate.—To undergo a change in genotypic character independently of normal segregation.

Ovule.—Female sex cell with its immediate surrounding parts.

Ovum.—Egg cell.

P_1 , P_2 , Etc.—The first, second, etc. generation of the parents.

Palea.—The upper of the two bracts immediately enclosing each floret in grasses.

Panicle.—A compound inflorescence with pediceled flowers usually loose and irregular, as in oats, rice, proso, etc.

Pedicel.—A stalk on which an individual blossom is borne.

Peduncle.—The primary stalk supporting either an inflorescence or a solitary flower. In grasses the uppermost internode of the culm.

Pericarp.—The matured wall of the ovary.

Phenotype.—The apparent type of an individual or group of individuals, *i.e.* the sum of the externally obvious characteristics which an individual possesses, or which a group of individuals possess in common; contrasted with genotype.

Presence and Absence Hypothesis.—The hypothesis that any simple Mendelian difference between individuals, results solely from the presence of a factor in the genotype of the one individual, which is absent from that of the other. Presence and absence of unit-differences as a convenient *method* of describing the results of genetic experiments should be carefully distinguished from the presence and absence hypothesis. The *method* is purely objective and entirely free from hypothetical implications.

Probable Error.—A measure of accuracy for results obtained by statistical methods. The chances are even that the true value lies within the limits marked by the probable error.

Probable Error of a Single Determination.— $S. D. \times \pm 0.6745$.

Pubescent.—Hairy in a general sense; in special use, covered with short, soft hairs.

Pure Line.—A group of individuals derived solely by one or more self-fertilizations from a common homozygous ancestor. Sometimes erroneously applied to groups of individuals believed to be genotypically homogeneous (a homozygous biotype or a clone) without regard to the method of reproduction.

Recombination.—Union of parental factors in individuals of the second or later generations after a cross.

Reduction Division.—That in which homologous chromosomes separate preparatory to formation of gametes.

Repulsion.—Such a relation between two genetic factors that both are not, as a rule, included in the same gamete, referring especially to cases in which the factors in question give rise to obviously different characteristics; also called "spurious allelomorphism."

Replication.—Systematic repetition. Used in field work to designate the systematic distribution of plots of each strain or variety to overcome soil heterogeneity. Two replications means the use of three plots systematically distributed.

Roguing.—The act of removing undesirable individuals from a varietal mixture in the field by hand selection.

Seed.—The mature ovule, consisting of the kernel and its proper coat.

Self-fertilization.—The union of the egg cell of one individual with the sperm cell of the same individual.

Self-sterility.—That condition in which the male gametes of an organism are incapable of fertilizing the female gametes of the same individual.

Segregate.—With reference to Mendelian characters, to become separated through the independent distribution of the genetic factors before or at the time of the formation of the gametes.

Sex-linked Inheritance.—The association of the determiner for any unit-character with a sex-determiner, in such a manner that the two determiners are either generally included in the same gamete, or that they are generally included in different gametes.

Somatic Segregation.—Segregation during somatic division.

Species.—A group of varieties or a single variety which in botanical characters and genetic relationship can be differentiated from another group or variety belonging to the same genus or to other genera.

Spikelet.—A small or secondary spike, especially in the inflorescence of grasses.

Spike.—A simple inflorescence with the flowers sessile or nearly so on a more or less elongated common axis or rachis.

Sperm or Sperm Cell.—Male sex-cell.

Standard Deviation.—An absolute measurement of variation in terms of the mean. The square root of the sum of the deviations squared divided by the number of variates.

Sterility.—Inability to reproduce; when male and female gametes, through incompatibility or some other cause, are incapable of mating or fertilization.

Strain.—A group within a variety which constantly differs in genetic factors or a single genetic factor difference from other strains of the same variety.

Tassel.—Used to designate the staminate inflorescence of maize.

Unit-character.—In Mendelian inheritance, a character or alternative difference of any kind, which is either present or absent, as a whole, in each individual, and which is capable of becoming associated in new combinations with other unit-characters.

Variate.—A single magnitude determination of a character.

Variety.—A group of strains or a single strain which, by its structural or functional characters, can be differentiated from another variety.

Variety Group.—A complex of varieties which resemble each other more than varieties belonging to a different group. Of lower grade than species.

Xenia.—The apparent immediate effect of pollen. It results from double fertilization.

Zygote.—The body formed by the union of two gametes and containing $2c$ number of chromosomes.

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